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The Genus *Paradisaea*—Display and Evolution

MARY LECROY¹

ABSTRACT

The 42 species of birds of paradise are herein divided into three groups based on breeding behavior: one group of 12 species for which monogamy is known or assumed, one of 13 species which may either be territorial with a pair bond or polygynous with an "exploded" display arena, and one of 17 species presumed to be polygynous arena-displaying species without a pair bond. An attempt is made to list characteristics that are shared by arena birds but not necessarily restricted to them: (1) loud calls; (2) extreme sexual dimorphism in plumage; (3) males considerably larger than females; (4) few males in adult plumage seen in comparison to numbers of females and unplumed males; (5) groups of males displaying throughout much of the year whether or not females are present, and (6) frequently members of speciose genera.

The seven species of the genus *Paradisaea* are treated in greater detail. Six (*P. rubra*, *P. apoda*, *P. raggiana*, *P. minor*, *P. decora*, and *P. guilielmi*) are considered polygynous arena birds with

no pair bond. Reasons are given for thinking that *P. rudolphi* may have secondarily acquired pair bond behavior.

The known displays of the six polygynous arena species are analyzed and the importance of distinguishing between male-male displays which set up and maintain the male hierarchy and the female-male displays which lead to mating is stressed. I have recognized eight display postures in the genus: (1) Wing Pose; (2) Charging; (3) Zig-zagging; (4) Male-male Duetting; (5) Flower Display; (6) Inverted Display; (7) Hopping; and (8) Copulation. The first four are male-male displays; the last four are female-male displays.

Other display components are discussed: Bill-wiping, Pecking-at-Perch, Ritualized Preening, Leaf-plucking, Butterfly Dance, Sun-bathing, and Seed Regurgitation. Display of unplumed males is discussed, and a brief summary of calls is given. Evolution of polygyny and evolutionary relationships within the genus *Paradisaea* are discussed.

INTRODUCTION

Within the family Paradisaeidae, *Paradisaea* is the best-known genus. The seven species are birds of the lowlands and middle altitudes on New Guinea and nearby islands and may be found in close proximity to hu-

man settlement. Despite extensive collecting by local residents dating to long before European contact and a period of over-collecting for the European millinery trade in the late nineteenth and early twentieth centuries,

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the birds are numerous in areas where their habitat remains intact. Gilliard (1969) has discussed the reasons for this ability to withstand strong collecting pressures and has related them to the birds' mating system—an arena system in which males gather to display in groups, whether or not a female is present. Usually there is no pair bond formed, and females visit these assemblages of males only for copulation. Nesting and raising the young are carried out by the female alone.

My observations of *P. decora* (LeCroy, Kulupi, and Peckover, 1980), *P. minor*, *P. raggiana*, *P. guilielmi*, and *P. rudolphi* in the field, and a careful rereading of Gilliard's unpublished field journals and an unpublished manuscript on the birds of paradise and bowerbirds have led me to attempt the following analysis. My debt to Gilliard (1969, and other papers), Dinsmore (1969, 1970a, 1970b), and Cooper and Forshaw (1977) is obvious; and I have tried to consult as many original publications on these birds as possible.

Before beginning an analysis of mating behavior in the genus *Paradisaea*, I will attempt to place this genus within the wider context of mating behavior as it is currently known within the family. The following summary is based mainly on Gilliard (1969), Peckover (1973), and Cooper and Forshaw (1977).

BIRDS OF PARADISE KNOWN OR PRESUMED TO BE MONOGAMOUS

Of the 42 species of birds of paradise, 12 are either known to be or are suspected of being monogamous either due to lack of extreme sexual dimorphism or, in one case at least, because a domed nest is built and a brightly colored male would be concealed on the nest. These 12 species include the five species of *Manucodia* (including *keraudrenii*). *Manucodia ater* and *M. keraudrenii* males are known to assist with nesting (Rand, 1938; Cooper and Forshaw, 1977), and it is presumed that the other species do also. Of the mating of the *Paradigalla* superspecies (two species) nothing is known, but a pair bond is assumed because the sexes

are very similar and without bright colors or obvious displays. Nothing is known of *Lycocorax pyrrhopterus*, which is included here because of its dull coloration. Rand (1940) reported a male *Macgregoria pulchra* accompanying a female as she built a nest and when she left to feed while incubating, and helping to feed the young, thus indicating a pair bond.

The three species in the subfamily Cnemophilinae are little known and the information available is inconclusive. Gilliard (in Mayr and Gilliard, 1954) reported a male *Loria loriae* singing daily during July from a favorite perch; this possibly indicates territoriality. There is only moderate plumage dimorphism, both sexes being dull colored. In *Loboparadisea sericea* the male and female are similar and are brightly colored, but the yellow rump and underparts would not be visible in either sex if the bird were sitting on the nest. There is no further information on display or nesting. *Cnemophilus macgregoriae* shows extreme sexual dimorphism in plumage, with the male exhibiting an unusual "upside down" plumage pattern, red-orange on the upperparts and very dark brown below. However, it is included here because the species is known to travel in small parties of which one or two individuals are adult males, and these may be family parties. The observation that it builds a domed nest is usually given as a reason for considering that this species may have a pair bond, the conspicuous male thereby being effectively concealed if he visits the nest, but Loke (in Sims, 1956, p. 426, erroneously recorded under *Loria loriae*; see Gilliard, 1969, p. 89) saw only the female at the nest and feeding the young. This may indicate that there is no pair bond or only one of short duration. This nest was photographed by Loke (1957, and in Gyldenstolpe, 1955, pl. XI, erroneously identified as *Loria loriae*), and as W. S. Peckover (*in litt.*) has pointed out to me, the nest appears to be a hole in a living clump of moss and is thus not dissimilar to the nest reported for *Diphyllodes* (=*Cicinnurus*) *regius* in a cavity in a small tree (Gilliard, 1969, p. 199) and not truly a "domed" nest. Other birds of paradise may also nest in clumps of

vegetation. Local residents of Nade, Ferguson Island, said that *Paradisaea decora* put its nests in clumps of arboreal ferns. The nest of this species has not been collected, perhaps partly because collectors have not looked in such an "unusual" place for a *Paradisaea* nest.

SEXUALLY DIMORPHIC BIRDS OF PARADISE WITH UNDOCUMENTED BREEDING SYSTEMS

Thirteen of the dimorphic species are too poorly known for one to be able to decide whether the males are displaying territorially, in which case there may be a pair bond of greater or lesser duration and the female may nest within the male's territory; or whether an extreme form of arena behavior is involved and there is no pair bond, i.e., the "exploded" arena (Gilliard, 1963, pp. 41-42) where each male on his court is in auditory contact with other males but the arena is too large and the courts too far apart for males to be in visual contact. Presumably all 13 have either one or the other of these breeding systems, and there is potentially a thin line between a small territory and the courts of an exploded arena, in the latter case with the female not nesting within the territory and no pair bond formed. A "court" may be thought of as a very compressed territory. Details of these 13 species follow.

All three species of rifle birds are known for their loud calls and it may be that there is an exploded arena. The females are barred and cryptically colored, and the males are ornate with iridescent plumage and short flank plumes. Males of the three species are usually reported displaying alone in the tops of tall trees, but Sharland (1977) has reported a male *Ptiloris victoriae* displaying only 18 feet up on a broken off dead tree under the forest canopy and Coates (1973, p. 3) has reported a display between two males of *P. magnificus* in the forest understory. It is not known whether this was a territorial display nor is it known whether other males ever display within auditory range of solitary males displaying in tree tops.

In *Seleucidis melanoleuca* the male has elongated, brightly colored plumes and a loud call; the females are barred and cryptically colored. Males may be territorial as they are recorded displaying alone. At Kanganaman (Gilliard and LeCroy, 1966, p. 271) Gilliard found that the female alone incubated, but there is no information on whether this was within a male territory. Bergman (1957a, p. 19) records two female-plumaged birds visiting a male at his display tree, but later when he observed copulation only a single female was present.

The four species of sicklebills (*Epimachus*, including *Drepanornis*) are very poorly known. When displays have been seen they have been by males alone and loud calling by the males is noted in the four species. That females alone rear the young is possible as Gilliard (ms) and Cooper and Forshaw (1977, p. 107) independently saw a nesting female *Epimachus meyeri* chase a male *Astrapia mayeri* away from the nest vicinity and in neither case did a male *E. meyeri* appear.

Diamond (1972, p. 331) found altitudinal differences in distribution between males and females of *Lophorina superba* with both sexes occurring between 1550 and 1727 m., adult males only between 1727 and 2121 m., and females and immatures only between 1060 and 1550 m. Thane Pratt (personal commun.) found that female-plumaged birds occurred above and below, as well as throughout, the range of plumed males in his study area on Mt. Misim. The males were highly territorial, as was a male I observed near Ubaigubi, in the Eastern Highlands at approximately 1700 m., in October 1980. Diamond found that adult males were invariably solitary. However, in November 1978, Mary Stringer and I saw a male and a female-plumaged bird together flying in an open garden area just below undisturbed forest in the Kratke Mountains at about 1660 m., and in October 1980 near Ubaigubi I frequently saw a male and a female-plumaged bird of this species feeding together in second-growth and garden areas. In captivity a male fed and displayed to a nesting female but killed the young bird when it hatched. A second nest-

ing was successful as the male was removed (Timmis, 1968). Other observations indicating at least a short pair bond are allopreening by a captive pair (Crandall, 1932, p. 85) and a male coming to the aid of a female being chased out of a feeding tree by *Melipotes fumigatus* (Meliphagidae, Weston, 1977, p. 17).

Pteridophora alberti is apparently territorial with a male patrolling a territory and singing from various exposed perches (Gilliard, 1969, p. 188; Beach, 1975, p. 2), but males may clump in certain areas and there is thus the possibility that the territories serve as an exploded arena. The display with a female is a joint display in the substage of the forest canopy, and there is apparently no special display perch (Gilliard, 1969, p. 190; Beach, 1975, p. 2; Healey, 1975, pp. 6-7). There is no information on nest location and incubation.

The display of *Diphyllodes* (=*Cicinnurus*) *regius* in the wild is poorly known. Two males have been heard calling from the crowns of display trees 100 m. apart (Cooper and Forshaw, 1977, p. 162) and the display may have an aerial component (Goodfellow, in Ogilvie-Grant, 1915, p. 21). Whether this is arena display or territorial display is unknown. W. S. Peckover (*in litt.*) informs me that various members of the Papua New Guinea Bird Society, including himself, have observed a solitary male *D. regius* displaying in several localities near Port Moresby. In all of these cases there is "little doubt the displaying bird was in auditory contact with other 'nearby' displaying males." In captivity only the female tended the young and the male did not feed her (Bergman, 1957b).

Coates (in Cooper and Forshaw, 1977, p. 169) found that a male of *Diphyllodes magnificus* stationed himself on his main display perch and called loudly when another male was heard, but it is not known whether the other male was at a display area. However, Cooper and Mackay (in Cooper and Forshaw, 1977, p. 168) observed three female-plumaged birds at a display area; but when Mackay observed copulation there was only one female present. Also Thair and Thair (1977, p. 13) reported the presence of two

adult males at a display area. This may indicate that *Diphyllodes magnificus* has no pair bond and displays in an exploded arena and should be included in the following group. More information is needed. *Diphyllodes respublica* is little known in the wild but will presumably prove similar to *D. magnificus*.

SEXUALLY DIMORPHIC BIRDS OF PARADISE WITH ARENA BREEDING SYSTEMS

The remaining 17 species, except perhaps *Paradisaea rudolphi*, are probably arena-displaying birds without a pair bond and with a polygynous social system. There are a number of characteristics shared by arena birds but not necessarily restricted to them, and it is useful to list these before discussing the non-pair-bond-forming birds of paradise.

1. Loud calls: The ringing calls of males are frequently noted not only for arena-displaying birds of paradise but also for arena birds such as various species of manakins (Pipridae) and the Cock of the Rock (*Rupicola*) in South America. These calls probably serve the dual purpose of assembling males at a display arena and of informing females of display in progress. They may also serve to notify other groups of males of display activities of their neighbors. What little information we have on dispersal of arenas in a particular area indicates that activities at one arena are audible to birds at other arenas nearby (Peckover, personal commun., and LeCroy, personal observ.).

2. Extreme sexual dimorphism in plumage: As Gilliard (1969, p. 57) has stated, the release of males from nesting duties has apparently relaxed natural selection for cryptic coloration and allowed rapid selection for bright plumage coloration (presumably in response to agonistic displays among males). The unusually large number of hybrids between morphologically very distinct arena-displaying species argues for this, as genetic isolating mechanisms have not kept pace with the morphological changes in males. In these cases female plumage is usually cryptic and presumably conservative, although con-

vergence cannot be ruled out. The rapid and extreme development of sexual dimorphism of males is aided by the apparent fact that only a small percentage of the adult males in any clan are responsible for most of the matings. Thus changes occurring in the dominant male(s) are potentially passed on very quickly to most of the males in the population, assuming that these changes are advantageous in the setting up of a male dominance hierarchy. These easily recognized species-specific signals are also important to females, who rapidly mate and form no pair bond, for fast recognition of the correct male. Hybridization probably occurs when a female ready to mate is attracted to a display area of another species by the noise and movement of display among males. If the sort of altitudinal differences in distribution of the sexes that Diamond (1972) found in several species of bird of paradise is common, then it is easy to imagine a situation where males of one species are rare, but males of another species are more abundant. If a female ready to mate has difficulty finding a male of her own species, her threshold for discrimination may be lowered and mating with the wrong species might occur quickly upon her arrival at the arena.

3. Males considerably larger than females: This frequently occurs in arena birds and is presumably due to the same sort of selection pressures that allow for elaborate plume development in males. Upper limits of size differences in the sexes are presumably set by genetic constraints of mating compatibility, egg size, development of the embryo, and the ability of the female to raise the young. The size differences are apparent even in unplumed males (see table 1).

4. Few males in adult plumage compared with the number of unplumed males and females seen: This, along with the possibility of a different altitudinal distribution of the sexes at certain times of the year, leads to an apparent skewed sex ratio; many accounts of arena birds stress the scarcity of males. This has been proposed as an explanation for the development of arena display by Darwin and others, but it seems clear now that this apparent scarcity of males is a result

of the arena system, not its cause. There is the possibility (discussed below) that plume development in subordinate males may be inhibited.

5. Groups of males display for long periods during the year in arenas or exploded arenas, with or without females present: This has to do with the setting up and maintenance of the male-male hierarchy and is discussed more fully below.

6. Frequently associated with speciose genera: This may be assumed to have come about as an extension of the rapid acquisition of sexual dimorphism. Isolation of populations would lead to rapid differentiation. In birds of paradise the arena birds are the genera that have speciated most.

The 17 arena-displaying species of Paradisaeidae are in only four genera. *Semioptera wallacei* is a monotypic genus and is confined to Halmahera and Batjan, with a subspecies on each island. It is very little known, but Gilliard (1969) gives evidence that it is an arena bird with groups of males displaying in low slender trees close together, that unplumed males and females outnumber plumed males, that it has a harsh call, and that there is some sexual dimorphism in size.

The remaining species are in three genera: *Astrapia*, *Parotia*, and *Paradisaea*. Healey (1978b) has recently described the communal display of *Astrapia stephaniae*. He gives distribution of display arenas, description of arenas (exploded arenas composed of several nearby trees), differing altitudinal distribution of males and female-plumaged birds (2050–2250 m. for all plumages but female-plumaged birds down to 1630 m. on occasion), reports virtually year-long period of display by males, and mentions loud calls and whistles by males at the display site but virtually silent displays to females. In all of these traits *A. stephaniae* agrees with other arena species.

The other species of *Astrapia*, except perhaps *A. splendidissima*, will probably also prove to have communal displays. All five species are sexually dimorphic in plumage and all except *splendidissima* have pronounced sexual dimorphism in size. Differ-

TABLE 1
Measurements (in Millimeters) of the Genus *Paradisaea*

	Wing		Tail		Exposed Bill		Tarsus		Weights	
	Range (mean \pm SD)	N	Range (mean \pm SD)	N	Range (mean \pm SD)	N	Range (mean \pm SD)	N	Range (mean \pm SD)	N
<i>Paradisaea apoda</i>										
<i>apoda</i>										
Plumed males	222.0–232.0 (227.6 \pm 3.8)	5	156.5–171.0 (162.2 \pm 4.8)	6	34.0–36.0 (35.3 \pm 1.0)	4	53.0–57.0 (55.2 \pm 1.5)	6	—	—
Unplumed males	196.0–231.0 (213.9 \pm 12.9)	7	141.0–162.0 (153.3 \pm 6.9)	7	35.0–39.0 (36.6 \pm 1.4)	7	52.5–56.0 (54.3 \pm 1.3)	7	—	—
Females	178.0–190.0 (183.3 \pm 5.4)	4	132.0–137.0 (134.5 \pm 2.4)	4	33.5–36.0 (34.9 \pm 1.3)	4	47.0–49.0 (47.9 \pm 1.0)	4	—	—
<i>novaeguineae</i>										
Plumed males	195.0–209.0 (199.4 \pm 5.1)	9	133.0–153.0 (141.0 \pm 5.3)	13	31.0–34.0 (32.3 \pm 0.8)	12	46.0–51.5 (48.3 \pm 2.2)	5	—	—
Unplumed males	180.0–197.0 (186.8 \pm 7.5)	5	131.0–141.5 (136.5 \pm 4.5)	5	32.0–34.0 (32.6 \pm 1.0)	4	49.0–50.0 (49.7 \pm 0.5)	5	—	—
Females	169.0–175.0 (171.0 \pm 3.5)	3	126.0–133.0 (128.7 \pm 3.8)	3	32.0–34.0 (32.7 \pm 1.2)	3	41.0–44.0 (42.0 \pm 1.7)	3	170.0, 173.02	2
<i>Paradisaea raggiana</i>										
<i>salvadorii</i>										
Plumed males	183.0–194.0 (187.3 \pm 4.1)	8	129.0–142.0 (132.9 \pm 4.2)	8	31.0–33.5 (32.1 \pm 0.9)	8	42.0–47.0 (45.2 \pm 1.7)	7	—	—
Unplumed males	173.0–191.0 (181.1 \pm 4.8)	21	120.0–140.0 (129.7 \pm 5.7)	20	31.0–35.0 (32.4 \pm 1.1)	19	43.0–49.0 (45.6 \pm 1.6)	20	—	—
Females	149.0–169.0 (160.0 \pm 5.8)	13	112.0–125.0 (118.0 \pm 4.5)	13	30.0–33.0 (31.5 \pm 0.9)	13	38.0–44.0 (40.0 \pm 1.9)	12	168.0–203.0 (187.3 \pm 17.8)	3
<i>raggiana</i>										
Plumed males	178.0–199.0 (188.4 \pm 5.4)	24	127.0–144.0 (135.6 \pm 4.7)	23	30.0–33.5 (31.9 \pm 0.9)	20	44.0–48.0 (46.4 \pm 1.0)	22	—	—
Unplumed males	187.0, 190.0	2	135.0, 142.0	2	32.0, 32.0	2	47.0	1	—	—
Females	156.0–164.0 (159.0 \pm 3.1)	5	116.0–121.5 (118.9 \pm 2.3)	5	30.0–33.0 (31.5 \pm 1.2)	5	39.0–41.0 (40.4 \pm 0.9)	5	—	—
<i>intermedia</i>										
Plumed males	177.0–188.0 (183.1 \pm 4.0)	12	127.0–140.0 (131.7 \pm 3.9)	11	31.0–35.0 (32.4 \pm 1.1)	11	42.0–47.0 (45.3 \pm 1.6)	11	—	—
Unplumed males	166.0–186.0 (177.5 \pm 6.7)	11	122.0–134.0 (128.5 \pm 4.0)	10	32.0–34.0 (33.2 \pm 1.0)	9	42.0–46.0 (44.9 \pm 1.3)	11	—	—
Females	151.0–159.0 (157.9 \pm 3.4)	7	113.0–128.0 (119.0 \pm 5.3)	7	32.0–33.5 (32.6 \pm 0.6)	7	38.0–41.0 (39.0 \pm 1.2)	7	—	—
<i>augustaevictoriae</i>										
Plumed males	184.0–192.0 (188.4 \pm 2.0)	18	127.0–138.0 (133.3 \pm 3.3)	17	31.0–35.5 (32.8 \pm 1.2)	16	44.5–49.0 (46.8 \pm 1.2)	18	—	—
Unplumed males	175.0–187.0 (183.2 \pm 4.8)	5	122.0–138.0 (130.6 \pm 6.0)	5	33.0–34.0 (33.4 \pm 0.6)	5	45.0–48.0 (47.0 \pm 1.2)	5	—	—
Females	150.0–168.0 (159.2 \pm 4.6)	12	111.0–123.0 (115.8 \pm 3.5)	12	31.0–34.0 (32.5 \pm 0.9)	10	39.0–42.0 (40.2 \pm 1.0)	12	—	—

TABLE 1—(Continued)

	Wing		Tail		Exposed Bill		Tarsus		Weights	
	Range (mean \pm SD)	N	Range (mean \pm SD)	N	Range (mean \pm SD)	N	Range (mean \pm SD)	N	Range (mean \pm SD)	N
<i>Paradisaea minor</i>										
<i>finschi</i>										
Plumed males	185.0–197.0 (192.5 \pm 2.9)	12	127.0–141.0 (134.8 \pm 4.0)	12	32.0–34.0 (32.9 \pm 0.7)	10	47.0–50.0 (48.0 \pm 0.9)	12	264.0–291.0 (278.6 \pm 10.7)	5
Unplumed males	175.0–191.0 (184.3 \pm 5.9)	5	124.5–134.0 (131.3 \pm 3.9)	5	32.0–34.0 (33.0 \pm 0.6)	6	48.0–50.0 (49.2 \pm 0.7)	6	256.0, 268.0	2
Females	156.0–167.0 (161.2 \pm 5.1)	6	113.0–121.0 (116.0 \pm 3.5)	6	31.0–34.0 (32.2 \pm 1.0)	6	40.0–43.0 (42.0 \pm 1.0)	6	185.0	1
<i>jobiensis</i>										
Plumed males	198.0–204.0 (201.6 \pm 2.5)	5	137.0–143.0 (140.3 \pm 2.7)	6	33.5–36.0 (34.3 \pm 1.2)	5	50.0–53.0 (51.4 \pm 1.5)	5	293.0, 300.0	2
Unplumed males	181.0–192.0 (186.3 \pm 5.5)	3	130.0–139.0 (133.7 \pm 4.7)	3	33.0–34.0 (33.7 \pm 0.6)	5	49.0–53.0 (51.3 \pm 2.1)	3	210.0, 250.0	2
Females	161.0–179.0 (169.2 \pm 6.2)	6	119.0–129.0 (122.8 \pm 5.2)	5	31.0–33.5 (33.3 \pm 0.9)	6	43.0–45.0 (44.3 \pm 0.8)	6	152.0, 185.0	2
<i>minor</i>										
Plumed males	178.0–195.0 (185.7 \pm 4.8)	19	120.0–137.0 (128.6 \pm 4.5)	19	30.0–35.5 (33.1 \pm 1.6)	19	45.0–51.5 (47.2 \pm 1.4)	19	225.0–285.0 (250.0 \pm 22.9)	5
Unplumed males	172.0–186.0 (177.7 \pm 4.0)	16	119.0–130.0 (124.6 \pm 3.5)	18	32.0–34.0 (33.3 \pm 0.7)	19	44.0–50.0 (46.8 \pm 1.6)	19	205.0	1
Females	155.0–165.0 (159.3 \pm 3.1)	14	110.0–119.0 (114.4 \pm 3.1)	14	31.0–36.0 (32.4 \pm 1.3)	18	38.5–44.0 (41.6 \pm 1.2)	18	165.0, 170.0	2
<i>"pulchra"</i>										
Plumed males	190.0–192.0 (190.7 \pm 1.15)	3	130.0–132.0 (131.0 \pm 1.0)	3	32.5–33.0 (32.8 \pm 0.3)	3	46.5–48.0 (47.2 \pm 0.8)	3	—	—
Unplumed males	176.0–194.0 (184 \pm 9.2)	3	120.0–134.0 (129.0 \pm 7.8)	3	33.0–34.5 (33.8 \pm 0.8)	3	44.0–48.0 (46.5 \pm 2.2)	3	—	—
Females	161.0–168.0 (164.3 \pm 2.9)	4	106.0–116.0 (109.5 \pm 4.5)	4	32.0–34.0 (33.0 \pm 0.8)	4	40.0–42.0 (41.4 \pm 0.9)	4	—	—
<i>Paradisaea decora</i>										
Plumed males	176.0–182.0 (180.0 \pm 2.0)	9	134.0–144.0 (138.5 \pm 2.9)	8	33.5–35.0 (33.9 \pm 0.5)	8	42.0–46.0 (43.7 \pm 1.2)	9	237.0	1
Unplumed males	174.0–182.0 (177.1 \pm 2.5)	9	136.0–145.5 (139.9 \pm 3.4)	9	33.0–34.5 (33.4 \pm 0.6)	8	42.0–44.5 (43.1 \pm 0.6)	9	—	—
Females	156.0–165.0 (159.2 \pm 4.0)	4	124.0–130.0 (128.3 \pm 2.9)	4	32.0–34.0 (32.9 \pm 1.0)	4	38.0–39.0 (38.5 \pm 0.6)	4	—	—
<i>Paradisaea rubra</i>										
Plumed males	171.0–178.0 (174.1 \pm 2.1)	14	115.5–126.0 (120.3 \pm 3.3)	17	27.0–29.0 (28.4 \pm 0.8)	15	43.0–45.0 (44.1 \pm 0.6)	15	158.0–224.0 (203.7 \pm 20.3)	8
Unplumed males	166.0–174.0 (170.8 \pm 3.2)	15	113.0–127.0 (120.1 \pm 3.6)	15	25.0–30.0 (28.1 \pm 1.4)	14	42.0–45.0 (43.8 \pm 1.0)	15	156.0–212.0 (194.9 \pm 19.2)	8
Females	150.0–160.0 (154.0 \pm 4.2)	9	107.5–114.0 (110.8 \pm 2.7)	8	28.5–32.0 (30.9 \pm 1.1)	9	39.0–42.5 (40.5 \pm 1.3)	8	137.0–182.0 (156.8 \pm 17.0)	5

TABLE 1—(Continued)

	Wing		Tail		Exposed Bill		Tarsus		Weights	
	Range (mean ± SD)	N	Range (mean ± SD)	N	Range (mean ± SD)	N	Range (mean ± SD)	N	Range (mean ± SD)	N
<i>Paradisaea guilielmi</i>										
Plumed males	169.0–181.0 (174.8 ± 3.1)	16	109.0–120.0 (115.4 ± 3.6)	16	34.5–38.0 (36.7 ± 1.2)	16	45.0–48.0 (46.6 ± 0.9)	17	—	—
Unplumed males	161.0–183.0 (171.6 ± 6.0)	10	111.0–120.0 (115.0 ± 2.8)	11	36.0–40.0 (37.4 ± 1.2)	11	44.5–49.0 (46.5 ± 1.4)	11	—	—
Females	150.0–157.0 (153.8 ± 2.7)	7	101.0–110.0 (104.2 ± 3.0)	7	34.5–36.0 (35.5 ± 0.7)	7	40.0–42.0 (41.4 ± 0.9)	7	—	—
<i>Paradisaea rudolphi</i>										
Plumed males	152.0–160.0 (157.2 ± 3.1)	6	76.0–80.0 (78.6 ± 2.6)	6	31.0–34.0 (32.3 ± 1.0)	6	40.5–43.0 (42.3 ± 1.0)	6	178.0	1
Unplumed males	153.0–156.0 (154.7 ± 1.5)	3	92.0–93.0 (92.3 ± 0.6)	3	33.0–34.0 (33.3 ± 0.6)	3	40.0–43.5 (42.2 ± 1.9)	3	165.0	1
Females	141.0–146.0 (143.0 ± 2.2)	4	91.0–100.0 (94.6 ± 3.6)	5	35.5–37.0 (36.3 ± 0.7)	5	37.0–41.0 (39.5 ± 2.0)	5	—	—
<i>margaretae</i>										
Unplumed male	153.0	1	98.5	1	34.0	1	40.0	1	—	—
Females	141.0, 147.0	2	94.0, 97.0	2	34.0, 34.0	2	39.0, 40.0	2	—	—
<i>ampla</i>										
Plumed male	152.0	1	76.0	1	30.0	1	43.0	1	—	—

ences between the displays of *A. stephaniae* seen by Healey and those reported by Crandall (1932) for captive *A. rothschildi* may prove to be at least partly the difference between male-male and female-male displays within the genus (see below for *Paradisaea*). In the geographically peripheral species (*A. nigra* and *A. rothschildi*) there has been no subspeciation but there is a cluster of populations on the main trunk of New Guinea that is similar to *Paradisaea* in distribution. *Astrapia mayeri* and *A. stephaniae* are broadly sympatric, and hybrids between these populations are known. It remains to be seen whether *A. stephaniae* and *A. splendidissima* meet.

The genus *Parotia* is composed of four species (five if one recognizes *helenae*, see Schodde and McKean, 1973). *Parotia wahnesi*, *P. sefilata*, and *P. lawesii* appear to have groups of courts in which groups of males display, and I would interpret this as an exploded arena system. However, I have watched a single male clear and display on three courts during a single display bout. During several days of observation there was never more than a single male present at the trio of courts. Very little is recorded con-

cerning calls. Displays are silent or virtually so, but calling occurs in the trees over a court. The sexes are very different in appearance and there is pronounced sexual dimorphism in size. In *P. carolae* and *P. sefilata*, adult males have been found to occur at higher altitudes than unplumed males and females. An apparent scarcity of males in adult plumage has been reported. While there are no known hybrids among the species, *P. lawesii* and *P. carolae* are at least locally sympatric and there is a recent report of a female-plumaged *P. lawesii* having been seen on a *P. carolae* court (Healey, 1976). The species occurring on the Vogelkop and on the Huon Peninsula have not subspeciated, but the central complex of populations has been considered to comprise two or three species with numerous subspecies. Again this is similar to the situation in *Paradisaea*. The seven currently recognized species of *Paradisaea* are discussed in detail below.

THE GENUS PARADISAEA

Paradisaea rubra and *P. decora* are island species and have not subspeciated. *P. apoda*

occurs on the Aru Islands and the adjacent mainland of New Guinea. The two subspecies of this species along with populations of *P. raggiana* and *P. minor* form a ring of intergrading subspecies circling New Guinea. Of the remaining two species *P. guilielmi* is monotypic and occurs on the Huon Peninsula, generally at higher elevations than *P. minor finschi* and *P. raggiana augustaevictoriae*. The details of its overlap with those two species are still unclear. It has been known to hybridize with both, and *P. guilielmi* and *P. raggiana* occur together in the Saruwaged Mts. (personal observ.). *Paradisaea rudolphi* is also generally confined to higher elevations in southeastern New Guinea; it has three subspecies. Little is known about its display, but it has hybridized with *P. raggiana*. The zones of intergradation involving these four species are narrow and limited in extent. Both *P. guilielmi* and *P. rudolphi* have a fully inverted display as a main component of their courtship, and this has presumably developed as an isolating mechanism in these species (Gilliard, 1969, p. 248).

Group displays by males are known in all species except *P. rudolphi*. All the other species have loud calls, extreme sexual dimorphism in plumage, pronounced sexual dimorphism in size (see table 1), and apparent paucity of plumed males with unplumed males and females being much more numerous, males displaying for most of the year, group displays by males in arenas or exploded arenas, no pair bond, and females nesting and raising the young entirely alone. *Paradisaea rudolphi* is poorly known but apparently its display differs so radically from the displays of the other six species that it will be discussed separately.

DISPLAY SYSTEMS

As each new description of a display is published it becomes more and more apparent that it is extremely important to distinguish between male-male encounters (including unplumed males, which can usually be identified on the basis of their large size and behavior) and female-male encounters. Gil-

liard (1969, p. 221) pointed out the importance of the distinction but had few descriptions of female-male encounters. The fact that sometimes one and sometimes the other has been described for a particular species or that unplumed males have been identified as females has led to what I believe is a false impression of species differences in displays.

MALE-MALE ENCOUNTERS: In male-male encounters the hierarchy within the clan is set up and maintained. Males display in groups, often, or perhaps usually, with unplumed males present.

Paradisaea apoda display has been very thoroughly studied by Gilliard (1958; 1969, pp. 399-414; and unpublished notes) and by Dinsmore (1970a, 1970b, and 1969) in a small, introduced population on Little Tobago in the West Indies. These birds apparently have an exploded arena composed of three or four trees. In Dinsmore's study, the three main trees were within 64 m. of each other; the fourth was less used and was farther away. There was usually one adult male per tree and one main display limb in that tree. But early in the season males came together and had a communal display, and this is presumably when the male-male hierarchy is set up. The small numbers of males in this introduced population would account for the differences between Gilliard's and Dinsmore's observations and those of Wallace (1869) in the Aru Islands. But Wallace obviously observed the communal display by males. He described a tree where both adult and unplumed males assembled "high up in the thickest of the foliage, and flying and jumping about so continually that I could get no good view of them." The display trees had "an immense head of spreading branches and large but scattered leaves, giving a clear space for the birds to play and exhibit their plumes. On one of these trees a dozen or twenty full-plumaged males assemble together" (Wallace, 1869).

Paradisaea decora also displays in an exploded arena of four (or five) trees 50 to 100 m. apart. Communal displays by males occur and up to four plumed and five unplumed males were present in one tree. During these group displays there was much activity in the

tree, with both plumed and unplumed birds actively displaying. Plumed males often chased unplumed males out of the tree but did not chase each other.

Frequently the males were distributed two plumed males per tree and these often dueted, and duetting could be heard simultaneously in other trees as well. Often there was loud calling back and forth between arena trees. The displays were noisy and rang through the forest (LeCroy, Kulupi, and Peckover, 1980).

Paradisaea raggiana salvadorii has an exploded arena in which three to six males display, usually one to a tree but sometimes several in a large tree. The arenas were 100 to approximately 400 feet in diameter. Each male appeared to own a display perch, generally a gently sloping limb under the canopy in tall slender trees 35–60 feet up, and these perches were from 20 to 50 or more feet apart (Gilliard, 1969). The individual display limbs are within auditory and visual range and when the owner of a limb is killed, that limb is deserted. In the one case Gilliard observed, an unplumed male came to the deserted limb after several days and displayed. No attack by plumed males was noted (Gilliard, ms).

But male-male encounters may bring several plumed and unplumed males into the area of a single male's display limb. When "a male with elaborate plumes, or even a male with long wires and no plumes, begins his deep calling, the drone of birds in female plumage [probably unplumed males] becomes excited and [converges] on the male making the best auditory rendition The drone moves from tree to tree, and a male which has won the attention of the drone one day may not necessarily win it again for several days to come." The male displays actively when these birds are around. "But he is most apt to be badgered by other males which select this critical time to leave their perches nearby and to investigate the commotion. They are probably stimulated by the performance, and they fly in close to the displaying male. This always causes a fight. The owner of the dance limb attacks the other males, especially those which land for a few

seconds at the edge of the dance limb. In attacking the intruding males the dance limb owner charges them from the center of the [display limb] and at such times his ornamental plumage is extended to its fullest . . . so that the position of the head of the charging bird is hard to determine." He chases first one and then another plumed male in this manner. This is accompanied by loud calling (Gilliard, ms).

Paradisaea minor finschi males display in five or six trees and then shift to other sets of trees nearby. There may be 5–15 males moving through the upper limbs, calling and displaying and there is no apparent defense of individual limbs by males. Loud calling was usually a sign of beginning display (Gilliard, ms). Bergman (in Gyldenstolpe, 1955) mentions a similar arrangement for *P. minor minor*, and Gilliard (1969, p. 235) says that the species "often performs its arena displays in the top of a single tree with the males dancing close together."

Gilliard (ms) noted that "the birds in female plumage [probably unplumed males] are all about in the crown and in the limbs close to the displaying males which perform together at the height of the ceremony without apparent competition. I have not seen copulation All I have seen is a group of males displaying together and I have seen this very well about five times, each time for a matter of hours. Some of these periods of observation began before daybreak, some were during the middle of the morning, some during the mid-afternoon and some terminated at dusk. Many times . . . I passed through the display area which bordered a main trail, or was within earshot of it, and during April and May, it was rare indeed when the display trees were not occupied by at least two birds."

Paradisaea guilielmi apparently displays in an exploded arena. Draffan (1978) found three areas where display took place, each consisting of three to four trees. Males moved from one group of trees to another, within sight and sound of each other. They finally settled in one or two trees to display in groups. He saw up to four males inverted simultaneously, with others in upright dis-

play nearby. Female plumaged birds (probably unplumed males) were watching them and hopping about the canopy. He also saw pairs or trios of plumed males displaying together.

Paradisaea rubra is little known in the wild. The description by Bergman (in Gyl- denstolpe, 1955) is the most complete. He reports a single giant display tree in a clearing with up to 10 males displaying on dead limbs high in the canopy. The birds were continually on the move from branch to branch "quivering with their ornamental plumes and rapidly beating the wings. While displaying they not only uttered their usual calls but also a number of other noises." There is no indication of whether there is limb ownership by a single male, nor did Bergman report the presence of unplumed males.

Gilliard, in his unpublished field notes from Batanta Island, says, "During afternoon, as during morning, tried to observe *Paradisaea rubra* in its display tree. I have now concluded that each adult male occupies a single tree at this season [June]. In morning I got under display tree but failed to see male. Tree is very tall and thickly leaved. In afternoon male was heard in same tree for more than one hour." This observation may indicate that after the group displays by males and the setting up of a male-male hierarchy, males may display singly, one to a tree.

It seems from the foregoing summaries that each species has communal male-male displays, differing in detail, in which the clan hierarchy is set up. It is not apparent, given the state of our knowledge at present, how males are incorporated into the hierarchy—i.e., whether subdominant males move up or males are recruited from unplumed males. Nor is it possible to know, in the absence of marked birds, how stable the hierarchy is or what percentage of copulations go to the dominant male(s), although Dinsmore (1970a, p. 318) reports that all copulations he observed in *P. apoda* on Little Tobago Island were by the same male, a bird identifiable in the field.

FEMALE-MALE ENCOUNTERS: Only in the

last few years have copulations been observed in *Paradisaea*. Gilliard (1969) and particularly Dinsmore (1970a) have both called attention to the basic differences between the female-male encounters and the male-male encounters. Copulation has been observed in the field in four species and these can be augmented with accounts of copulations in captivity. Male-male encounters are virtually never observed in captivity due to the fact that usually only single birds or a pair are acquired.

A common theme in the reports of male to female displays in *Paradisaea* is their static quality; whereas, there is much activity during male-male display. The position of the plumes may not change so that attention to details of plumage position without noting level of activity may fail to convey the extreme difference in effect between the two types of display.

Paradisaea apoda apoda: Dinsmore (1970a) described a male displaying in the presence of a female. There was only one male displaying and his movements included a static display (the "Flower Display" of Gilliard [1958, 1969]) and also a bouncing display. The female landed at the opposite end of the display limb and stood quietly and usually crouched. The male came toward her and extended his wing over her body while continuing to dance. The male rubbed his bill against the female's bill and the far side of her head and stretched his head and neck beneath hers. After about 20 seconds of dancing in contact, the male mounted. After copulation the female always flew out from under the male.

Paradisaea decora: Arrival of a female is announced by the male "growling." The male's movements are very slow and almost static and there are no vocalizations. A bouncing display may also be given. The male's plumes are raised until the shafts are vertical but the plumes do not fall forward over the head. The female stood quietly near the displaying male and then began soliciting by opening her wings slightly and quivering them. The male hopped stiffly up and down near the female, moved over to her and rubbed his chin and breast on her back and

put his wing over her briefly before mounting. He brought his wings down around her body while they copulated. Copulation lasted from 15 to 30 seconds (LeCroy, Kulipi, and Peckover, 1980).

Males frequently dueted in the presence of females, but one moved off to the side and sat quietly while the other courted and copulated with the female. More than one female may be present but additional females were not chased by the soliciting female, and once a male copulated with two females in quick succession. Unplumed males may be present and displaying and may copulate with the female (LeCroy, Kulipi, and Peckover, 1980).

Paradisaea raggiana: Female-male display may take several forms in this species, perhaps partly depending on whether the main display perch is vertical or horizontal. On a horizontal perch Gilliard (1969, p. 226) noted that the male is "silent and motionless except for the short upstrokes of the wings and the thudding sound of the wing-clapping, which is audible seventy feet away," and Crandall (1936, p. 98) saw a captive male tilting forward until the body was almost perpendicular to the perch. The wings were over the head and were brought together in the front, and the plumes were raised.

Cooper (in Cooper and Forshaw, 1977, p. 184) saw both of these displays with a female present and ending in copulation. "The female would sit beside or in front of the displaying male and reach in under the open wings to peck at his bill." The male mounted and they copulated repeatedly for four minutes. Cooper also noted that at least two plumed males were displaying on one perch but that one was dominant and chased away the other when a female was present. And once a female stopped soliciting to chase away another female.

David Gillison (personal commun.) has observed female-male display on a near vertical perch and in this situation the female perches above the male and they move together slowly up the perch with a ritualized bowing first to one side of the perch and then to the other. After about 30 seconds the male mounts the female while she is parallel to the limb. She turns crosswise of the limb and they copu-

late. The female then flies away. Prior to the female's arrival, two males had been dueting. The second male did not interfere with the female-male display, and several males crowded around the copulating couple again without interfering.

Paradisaea minor finschi: Gilliard (1969, p. 235) notes: "When [the female] was closest to him he was quite motionless, with the head held far down, much like the males of *Paradisaea apoda* of the Aru Islands in their 'flower' display." Gilliard also noted that the female arrived quietly. She pulled several times at the male's neck feathers but no copulation was attempted. Peckover (1973, p. 11) and Cooper and Forshaw (1977, p. 190) report that the wings of the male are over the female and display continues for a short while before the birds copulate.

Paradisaea guilielmi: Female-male display and copulation have not been observed.

Paradisaea rubra: Female-male display and copulation have not been observed.

It seems evident from the above brief summaries that female-male encounters are basically similar for the species for which we have information. The quiet behavior of the female, the static displays and lack of vocalizations by the male, the wing over the female and perhaps around her during copulation, and the billing or neck rubbing seem to be components of the displays in each species known.

DISPLAY POSTURES

Dinsmore (1970a) names five phases or display postures in *P. apoda* display. This is a convenient way to analyze the postures of the various species, and I have adopted some of his terminology but have subdivided one of his categories and added two others. I have also indicated male-male and female-male displays. Various earlier writers have also attempted to categorize display postures for different species, and I have tried to equate their categories with Dinsmore's whenever possible. Actual bouts of display often have certain postures repeated or omitted, particularly during bouts of male-male display with no female present, and the se-



FIG. 1. Wing Pose in *Paradisaea apoda*. New York Zoological Society Photo.

quence of postures given in any one bout is not necessarily in the order listed.

In the following account I include descriptions of display postures of both wild and captive birds. The postures in captive birds seem similar to those of wild birds. (Compare Gilliard's description of a wild *P. raggiana* Wing Pose given below to the photograph of a captive individual in figure 4.) However, the conditions under which the

displays are given are highly artificial and therefore the sequences of display, the context in which a display is given (male-male or female-male), and the orientation (position and height of display perch) may not be those normal to the species. Also we have almost no information on the range of normal display behavior in wild birds. Frith (MS) is convinced of the normality of sequences given by captive birds and discusses sequences



FIG. 2. Upright component of Wing Pose in *Paradisaea apoda*. Photograph by Frederick Kent Truslow, © National Geographic Society.

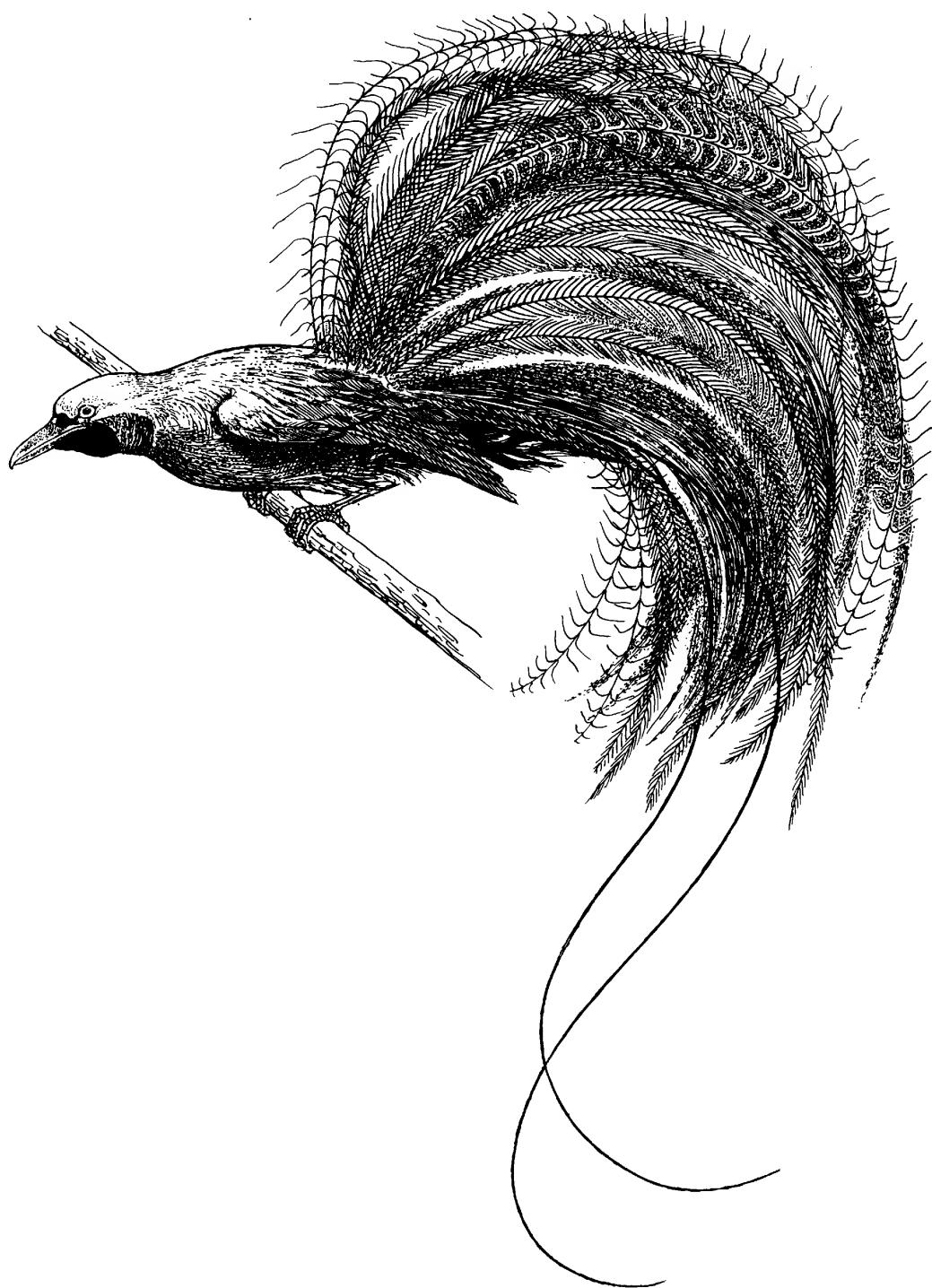


FIG. 3. Wing Pose in *Paradisaea decora*. Drawing by Juan Barbaris from a photograph by M. LeCroy.



FIG. 4. Wing Pose in *Paradisaea raggiana*, with wings over back. New York Zoological Society Photo.

of display in several species. This is another line of evidence and while some of our conclusions differ, we have independently reached similar conclusions in some cases.

WING POSE: This is essentially a male-male display although a female or females may be present. In *P. apoda apoda* the plumes are raised and the wings are to the front and down and held rigid (fig. 1); or the

male alternately drops the wings to his side and flaps them. The tail is tucked under the perch. This display is accompanied by loud "wauk" and "eee-ah" calls and may go on for 30 minutes or more. This corresponds to Crandall's (1936, pp. 90-91) first stage. There is also an upright component to the Wing Pose in *P. apoda apoda*, not mentioned, but photographed (fig. 2).



FIG. 5. Upright component of Wing Pose in *Paradisaea raggiana*. Photograph by Crawford H. Greenewalt.

This is essentially the same pose adopted by *P. decora* when several males are displaying together or two males are duetting. One male may also display alone in this manner. The wings are not brought so far forward; they are held more straight down to the sides of the body and moved with "rowing" motions. The tail and body remain more horizontal (fig. 3). This display may last for

30 minutes. Loud "wark" calls are given, or duetting males may give their ringing calls ending in "gargling." We did not observe an upright component of this posture in *P. decora* (LeCroy, Kulupi, and Peckover, 1980).

Gilliard (MS) describes this pose in *P. raggiana salvadorii* (fig. 4): "The dance begins when the male who has been sitting somewhat slouched on his perch suddenly deliv-



FIG. 6. Upright component of Wing Pose in *Paradisaea guilielmi*. Photograph by Crawford H. Greenewalt.

ers a loud bugled *Waa hee who whit*. This is punctuated with occasional *kees*, much

preening and bill wiping With body erect, he pulls the neck down silently in a



FIG. 7. Wing Pose in *Paradisaea raggiana* with wings down. Photograph by Crawford H. Greenewalt.

frontal crook with the bill straight ahead and a little elevated. Now he shuffles the wings a little and pulls them forward in such a way that they seem to become shortened. They are drawn high on the body with the shoulders pointed inward and hidden in the plumage of the neck. The primaries are opened and extended outward, the first primary extending forward almost to the eyes and standing free of the others in a peculiar manner. In this position the wings appear ridiculously short and assume the shape of fans framing the neck and head on the sides. Display begins silently with short waving of the wings. As this progresses the shoulders come close

together on the back. When excitement mounts a little further they come together with audible thumps over the upper back The upward movement of the shoulders is a snapping movement and the thumping of the wrists can be heard at a distance of fifty feet or more During this wing flapping the plumes are only partially spread and the plumes of the upper series are not much elevated over the level of the back." There is also an upright component in the Wing Pose of this species rather similar to that of *P. guilielmi* (figs. 5 and 6), and there is a position in which the wings are spread and down similar to the Wing Pose in *P.*

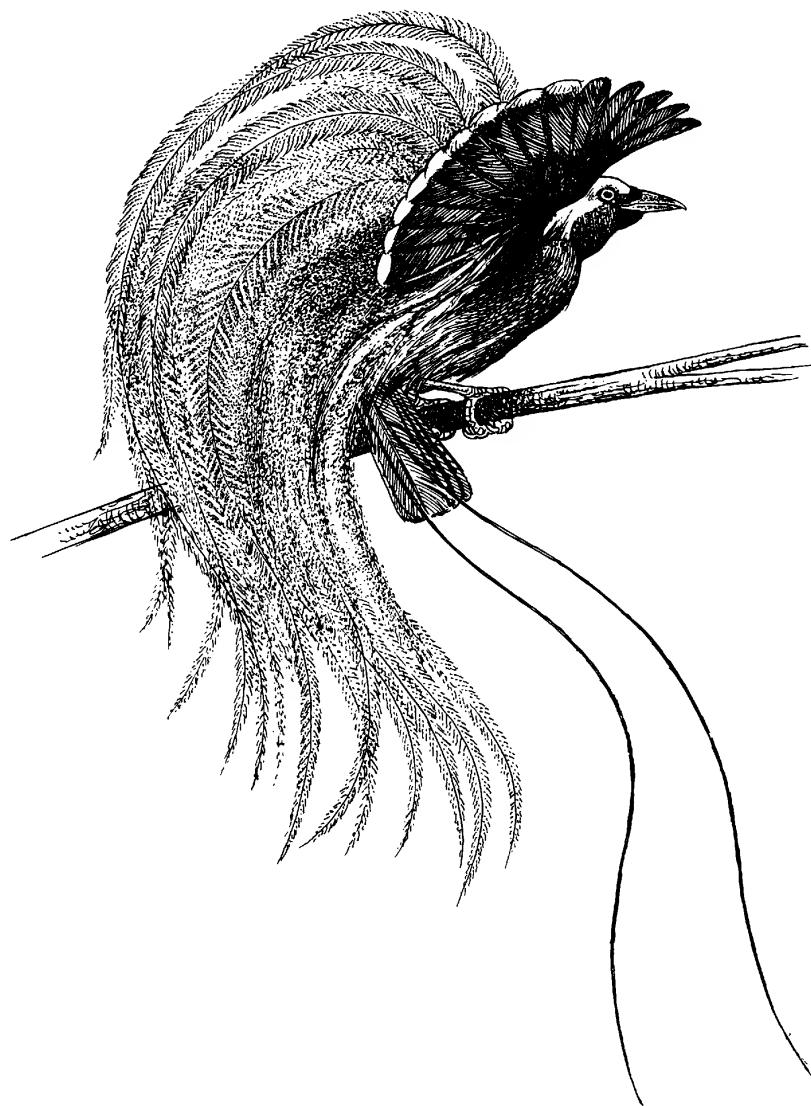


FIG. 8. Upright component of Wing Pose in *Paradisaea minor*. Drawing by Juan Barbaris after Ogilvie-Grant, 1905.

apoda apoda (fig. 7). *Paradisaea raggiana* is the only species so far reported to clap the wings together over the head, although the wings may be foreshortened in a similar way in *P. guilielmi* Wing Pose (fig. 6).

Paradisaea minor finschi: Gilliard (ms) noted that "The usual sign of beginning excitement was a clear series of rich notes, a ringing *gah haa haa waaaaaaah*, notes audible at least a quarter of a mile. Another

preliminary call is a sharp ringing *gig gig* and a sharp, plaintive *quee*. This is followed by much shaking of plumes in a kind of dusting motion and by side hopping. The head is held low and the body is moved in a near horizontal position with the neck crooked. As this is executed a low *grrrr* is emitted." Both Ogilvie-Grant (1905, p. 436) and Crandall (1936, p. 92) note that a captive bird was at first upright with the tail curved under the



FIG. 9. Charging in *Paradisaea apoda*. Photograph by E. T. Gilliard.

horizontal limb, wings open and held slightly above the level of the body, and the plumes arching upward (fig. 8). In both cases these birds were probably *P. m. minor*.

Paradisaea guilielmi: Stonor (1936, p. 1180) observed a captive bird displaying and described the beginning display as follows (fig. 6): "bird starts hopping up and down with head and neck stretched upwards; it then opens its wings and, jerking the head into the air, calls loudly several times with a clear and not unpleasing and very characteristic note."

"Next the wings are fluttered, with the head kept down, and during this part of the performance they are kept open for a few seconds and are then closed suddenly with a snap, this being repeated five or six times;

according to my own observations the plumes play no part in the performance."

Crandall (1932, p. 79) described the first part of the display in which the bird is bobbing slowly up and down from the hips with wings spread horizontally and vibrated rapidly and has plumes slightly raised. This display continued for about 10 minutes. Then the body became rigid and horizontal, the head and neck held forward and slightly down, and the flank plumes slightly raised. The wings were "suddenly spread and flicked forward, so that the upper surfaces were toward the bird's head." This position was held for about five seconds and then the wings were snapped back to their normal position for about five seconds. This was repeated seven times. These two accounts



FIG. 10. Charging in *Paradisaea raggiana*. Photograph by Crawford H. Greenewalt.

probably correspond to Group 1 of Wagner's (1938, p. 550) three groups of dances.

Draffan (1978, p. 158) "saw a couple [of males] displaying (not upside down) but with wings outstretched and quivering. They faced each other almost touching and then turned away from each other." This display may or may not prove homologous to the Wing Pose display.

Paradisaea rubra: Frith (1976, p. 70) stated that the male usually began by perching on a branch on or near the upper part of the vertical display limb. It "gives Bill-click-call frequently, flicks the outer primaries rapidly forward and back and occasionally performs Bill-wiping. Once on the vertical branch, he perches diagonally with bill pointing upward and continues to flick the primaries. As he becomes more excited the wings are slightly

spread and quivered; again he wipes his bill and sways gently from side to side."

CHARGING DISPLAY (The Pump Display of Dinsmore): In *P. a. apoda* this posture is assumed most often in male-male displays. The body is almost parallel to the display branch, the plumes are erected vertically and the head and bill are pointed down (fig. 9). The bird hops rapidly along the limb giving the "pump" call—a series of rapid *wa-wa-wa* notes—and bounding up and down. The movements are rapid and jerky (Dinsmore, 1970a, pp. 308-309).

Gilliard (1969, p. 219) noted: "Such jumps, charges, and cries are often synchronized between a number of males all calling and moving in a spasm of displays."

Paradisaea decora male or males perform this display on a horizontal branch, moving

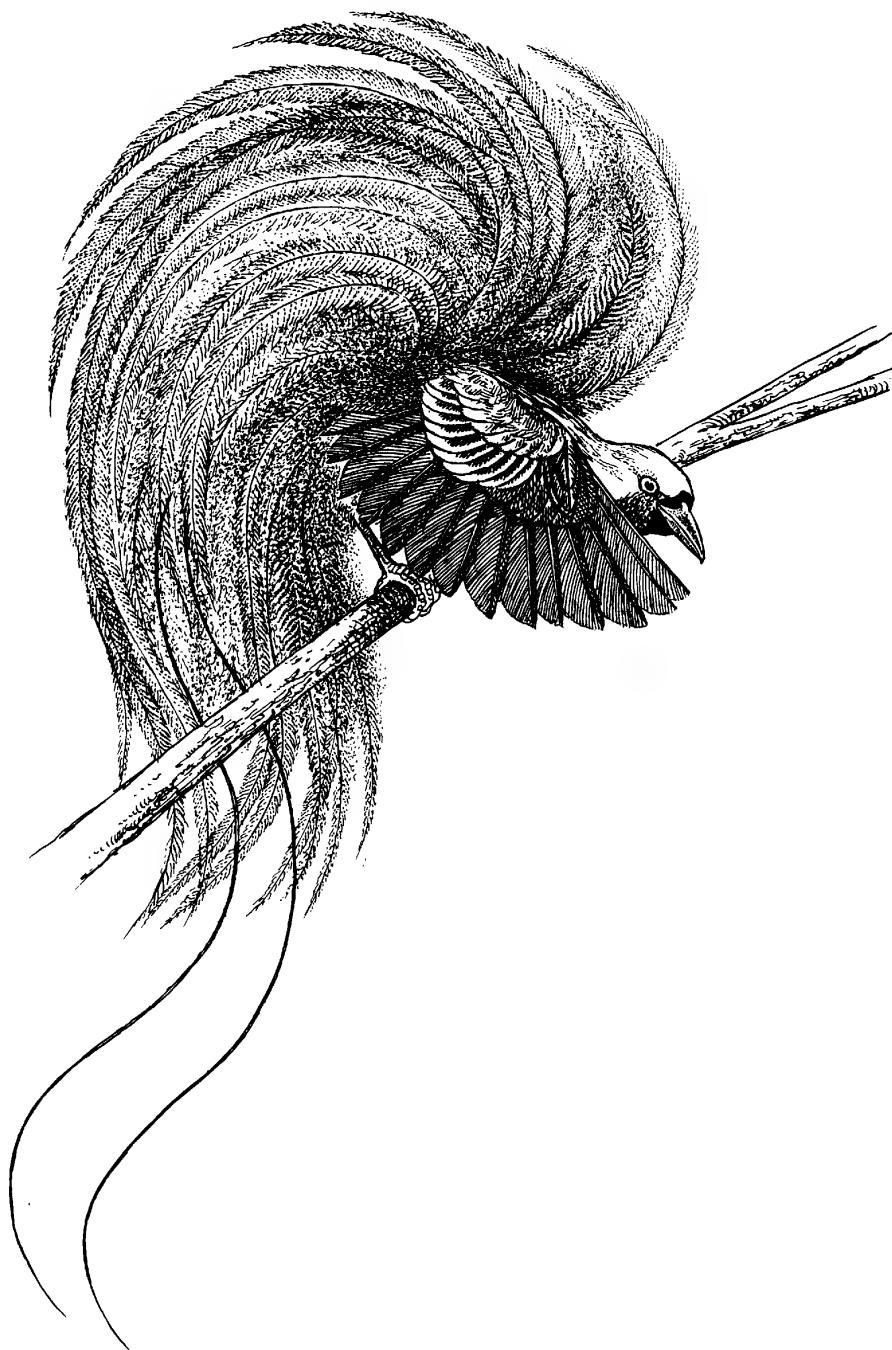


FIG. 11. Charging in *Paradisaea minor*. Drawing by Juan Barbaris after Ogilvie-Grant, 1905.

rapidly along the limb for several feet and then returning. The rowing motions of the wings may go below the level of the limb. Duetting birds may also adopt this pose and

move along adjacent limbs together (LeCroy, Kulupi, and Peckover, 1980).

In *P. raggiana salvadorii*, Gilliard (ms) also noted an active display of the same sort.

"The *quee, quee, quees* began which were repeated again and again in a rising crescendo. Later it took place again indicating that at least two males were dancing with their wings overhead and sort of charging each other slowly back and forth across the dance limb."

This display probably corresponds to the first stage of display given by Crandall (1936, pp. 95-98). The bird (fig. 10) calls loudly and runs on the horizontal perch with plumes whirling over the back and the body held horizontal. It may be given by a single individual or by two or more plumed males together.

Paradisaea minor: Bergman (in Gyldenstolpe, 1955, pp. 309-310) described this display: "After a few minutes they started to leap on the limbs uttering their harsh and rather penetrating guttural cries" The plumes were raised and the wings were jerked forward and quivered. There were "mock attacks" toward other displaying males. One tossed the head downwards, opened the bill and hopped to and fro on the branch. Ogilvie-Grant (1905, p. 438) also describes Charging in a captive male, in what he calls the second stage of display (fig. 11).

Paradisaea guilielmi: Crandall (1932, p. 79) spoke of a captive individual "moving about his perches" after having given the wing pose display. And Stonor (1936, p. 1181) said, "It may be noted that the dance is not at all unlike the typical *Paradisea* (sic.) display except that the plumes play no part." But it is not clear whether there is a Charging component in the display of this species.

Paradisaea rubra: I have not found a display reported in this species which seems homologous to Charging unless it is what Frith (1976, p. 73) called the Butterfly Dance. In this, males "hopped quickly from branch to branch with fluttering, flicking and extended wings like a butterfly and, suddenly landing on a vertical display-perch, went directly into the sequence with the inverted posture without preliminaries."

ZIGZAGGING: This component of display appears to be a part of male-male display. For *P. a. apoda*, Gilliard (unpublished notes, 1958) noted: On a perch at a 45 degree

angle a male became "very agitated, lowering the neck and head, and elevating the plumes. This male then 'switch-jumped' to a high perch and then pranced some more."

Paradisaea decora: The male performs this display on a nearly vertical branch. His body is parallel to the steeply sloping branch, and the rowing motions of his wings may go below the level of the limb. Changing the position of his feet as he moves up or down causes his body to appear to zigzag back and forth across the limb (personal observ.). Duetting birds may adopt this pose (see below).

Paradisaea raggiana salvadorii: Gilliard (MS) described this display thus: "The male danced in an area covering approximately six lineal feet of a steeply sloping limb. It walked up the limb and hopped down it sideways. [As it] walked up it moved lengthwise with the limb, placing one foot in front of the other, and walking very slowly, its wings partially opened and its plumes partially arranged to the side. This walk was slow and deliberate, and every foot or so the bird paused to posture by elevating the plumes somewhat and to . . . peck at the bark. At the top of the march the bird turned to the right and sat across the steeply pitched limb, then, in short hops it let itself down, as though jumping from stair to stair until it had again reached the bottom."

Again he (MS) noted: "Then suddenly [after the Wing Pose display] the bird delivers sharp *kei kei* notes, crooks the head deeply, leans low sometimes below the level of the feet and may hop several times switching the now erected, spread flank plumes from side to side of the perch as it switch-jumps along the perch or up a steep limb beside it. This serves to display the flank plumes."

David Gillison (personal commun.) has recently observed this rapid zigzagging display in *P. raggiana salvadorii* where three or four males may participate. It is to be distinguished from the slow, ritualized female-male display described below.

Paradisaea minor: I have not found Zigzagging described for this species.

Paradisaea guilielmi: No Zigzagging has been described for this species nor has any

vertical limb component, which may be necessary for this display to occur.

Paradisaea rubra: Frith (1976, p. 73) has noted that after the inverted display the plumage returns to normal and the plumed male hops down the nearly vertical perch, sometimes directly and sometimes in a spiral, and then back up, usually in a zigzag pattern. Crandall (1937, p. 194) noted that a bird of this species hopping up the slanting branch "leaped clear of the perch at each jump, alternating the feet in the forward position. This action caused the body to jerk violently from side to side, bringing the red plumes into greater prominence"

MALE-MALE DUETTING: Thorpe et al. (1972) have referred all cases of male-male dual song to "countersinging in defence of a territory or at a boundary." The synchronized calling of two *Paradisaea* males does not fit into this category. In these non-pair-bonding arena birds there is no territorial defense in the usual sense of the term, even if one accepts the hypothesis that display perches represent shrunken territories and that group calling may have evolved from male-male countersinging.

Group calling is a feature of the *Paradisaea* arena and two males' calling synchronously is probably only a special case of the more inclusive activity. Group calling probably helps in setting up and maintaining a hierarchy among males within the arena, particularly in exploded arenas, as well as in informing other males and females of the arena's location. Payne (1971) reports groups of males of parasitic cuckoos (*Cuculus solitarius*) calling together in a tree where females come when ready to mate. And many arena birds are well known for the loud calls of males on the display ground.

Foster (1977) discusses the synchronous calls of a pair of male *Chiroxiphia linearis* (Pipridae) that occupy a court and remain together, often for several years. These synchronous calls are not related to territory defense and Foster believes they serve to notify a female of an active court. I think the synchronized calling of two *Paradisaea* males is of this type. While there is as yet no evidence for or against a male-male bond in

Paradisaea, I think it is safe to say that the synchronized calling probably serves to maintain a dominance relationship between the two males and to attract females to an active display perch. Duetting is a useful term that accurately describes this activity and needs only to be designated Male-male Duetting to distinguish it from the male-female duetting discussed by Thorpe et al. (1972).

Male-male Duetting was first mentioned in *Paradisaea* by Dinsmore (1969, pp. 139-140) in *P. apoda*. In this species there were variations in the pattern of calls given by the two males and they did not seem to be a part of the courtship display although occasionally displays did follow duets. The duets that he heard involved two recognizable males on display limbs 46 m. apart, and he thinks that the dual calling may have evolved as a means of individual recognition between adjacent males.

A slightly different form of duetting in *P. apoda*, more like that in *P. decora*, was recorded by Gilliard (unpublished field notes, 1958): "The two began preening and flipping their wings and in a short time they were dancing together with their wings being expanded in the [rowing] position At one point I was particularly struck with the 'duality' of the display. That was when both males burst forth in a series of bugled notes that so perfectly overlapped that they could be mistaken for a series of notes from one bird and not two."

Paradisaea decora has the most elaborate Male-male Duetting so far reported (LeCroy, Kulupi, and Peckover, 1980). Pairs of males apparently share a display tree and the duetting probably serves to set up a dominance hierarchy between them. This seems especially likely in the light of the fact that one male of the pair sits quietly when the other is displaying to, and copulating with, a female. Male-male Duetting has become an important display component in this species and the loud, ringing metallic calls and "gargling" are characteristic sounds of displaying birds in the forests of Fergusson Island.

There is no published record of Male-male Duetting in *P. raggiana*, but W. S. Peckover



FIG. 12. Two male *Paradisaea raggiana* displaying together. Photograph by David Gillison.



FIG. 13. Flower Display in *Paradisaea apoda*. Photograph by Frederick Kent Truslow, © National Geographic Society.

has recorded what is undoubtedly such duetting at Varirata National Park near Port Moresby and Peckover and I observed it in October 1980. Also David Gillison (personal commun.) tells me that two or more males frequently display and call together. Cooper (in Cooper and Forshaw, 1977, p. 184) reported: "There were at least two fully plumed males using the display perch, one obviously dominant because it always chased off the second male whenever a female appeared." And I have seen photo-

graphs by David Gillison (fig. 12) and David Parer showing two males displaying together.

I find no record of possible Male-male Duetting behavior in *P. minor*.

Both Wagner (1938) and Draffan (1978) give evidence of pairs of captive and wild males of *P. guilieimi* displaying together. Draffan "saw [two males] displaying (not upside down) but with wings outstretched and quivering. They faced each other almost touching and then turned away from each

other." Wagner describes a similar display but neither author comments on any vocalizations. In November 1979, I watched two males give a bubbling duet in the Saruwaged Mts. However, this was an isolated occurrence and it remains to be seen how it fits into the species' display sequence.

Frith (1976) does not mention Male-male Duetting in *P. rubra*.

FLOWER DISPLAY: Dinsmore (1970a, p. 309) calls this the Bow and describes it for *P. apoda*, and it is illustrated by Truslow (in Gilliard, 1958, see also fig. 13). In this display the body is humped with both head and tail low, the wings are out and cupped around the limb and the plumes are erect over the back and extend forward over the head as well in a golden spray. A female may or may not be present and a *baa* note may be given as the bird tips its body down. If the female is present the display may be held for over a minute.

This is the display described by Crandall (1936, p. 91) as "Full Display," by Wallace (1869), and by Gilliard (1958) as the Flower Display.

Paradisaea decora: In this species this static display is less extreme. The body remains virtually horizontal and while the plumes are erected vertically, they were never seen to fall forward over the head. The bird was usually silent, although loud *whick-whick* calls were occasionally given. The rowing motion of the wings continued spasmodically. The Flower Display may occur when no female is present but is more prolonged when the female is there.

Paradisaea raggiana salvadorii: Gilliard (1969, p. 98) described this display, in which the male crouched forward, elevated and expanded the plumes and clapped the wings together over the head. The display was silent and motionless except for the upstrokes of the wings and the sound of the wing clapping. This is also the "Full Display" of Crandall (1936, p. 98).

Paradisaea minor minor: Crandall (1936, pp. 92-94) describes the "Full Display" in which the male holds the wings horizontal or curves them downward as does *P. apoda*. The body is arched downward but not so low

as in *P. apoda* and the plumes are up. The display of *P. minor finschi* reminded Gilliard (1969, p. 235) of the Flower Display of *P. apoda*. He described the peculiar manner in which the wings are held (Gilliard, ms): "The shoulders are drawn close to the body and the primaries are extended outward, almost straight out like an oarsman holding oars out of the water. They are held still for a while, and the bird makes no noise except the occasional low *graaa*. Then the wings begin to move up and down, moving up slowly about three inches at their tips, then downward snappily to a point just below the shoulders . . . as the performance continues, [the flank plumes] begin to rise up behind in a splendid cascade. But the distinctive thing is that certain of the shorter yellow flank plumes are lofted through the opening normally covered by the scapulars, and they stick up in random places like separate little golden fountains."

Ogilvie-Grant (1905, p. 438) mentions a static phase following Charging: "For some seconds he remains in a sort of ecstasy, rubbing his bill on the perch, and occasionally glancing backwards below his feet with the back fully arched" (fig. 14).

A female may or may not be present.

Paradisaea guilielmi and *P. rubra*: I have found no description of a static Flower Display in these species.

INVERTED DISPLAY: As *Paradisaea* is studied more, it becomes increasingly likely that an Inverted Display occurs in all species. It is only in *P. guilielmi* (and *P. rudolphi*) that it is developed to its fullest extent. In these two species it is a static display and probably serves as an isolating mechanism. In all species of *Paradisaea* the static displays are the most obvious component of female-male displays and probably serve as species specific signals. The two species of *Paradisaea* that have developed the Inverted Display most fully overlap in distribution other *Paradisaea* species and would thus most need an isolating mechanism to prevent the hybridization known to occur occasionally.

Paradisaea apoda apoda: Dinsmore (1970a, p. 312) noted a male hanging briefly upside



FIG. 14. Flower Display in *Paradisaea minor*. Drawing by Juan Barbaris after Ogilvie-Grant, 1905.



FIG. 15. Inverted posture in *Paradisaea raggiana*. New York Zoological Society Photo.

down on five different occasions, shortly after a bout of display. This was accompanied by nasal calls. Once a male briefly hung up-

side down while another male was displaying nearby. He considered that it was not a regular component of display in this species.



FIG. 16. Inverted posture in *Paradisaea minor*. New York Zoological Society Photo.

Paradisaea decora: This species has not been observed in an inverted posture.

Paradisaea raggiana salvadorii: Crandall (1936, p. 98) noted and gave a photo of this species in full display with head forward and down below the level of the branch (fig. 15). It is apparently common during most intense display. Opit (1975), Hadden (1976), and Cooper (in Cooper and Forshaw, 1977, p. 184) also saw a male display in an inverted position.

Gilliard (ms) noted: "An excited male happened to fall over and hang upside down, his head pointing toward the ground and waving like a slow-moving pendulum, as though trying to gauge its drop if it fell. After sev-

eral seconds of this with the plumes fanned out, a bird in female plumage dove in and landed on the center of the display perch directly over the feet of the hanging male, so close that their feet must have touched. This brought on an instantaneous fencing match as the suspended male attempted to fight his way to an upright position. This was seen only once"

Another time (Gilliard, ms) an unplumed bird was charged by a plumed male, fell backward and hung upside down for about 30 seconds with the male standing almost directly over the inverted bird.

Paradisaea minor: The only mention of an inverted display that I have found is in Elliot

(1873). He quotes Mr. A. D. Bartlett, Superintendent of Zoological Gardens, Regents Park: "During this display the bird would become greatly excited, and sometimes turn almost under the perch or branch, the head and neck being bent so low down." Also Crandall photographed a male in inverted position (fig. 16) but did not mention this in his paper.

Paradisaea guilielmi: Crandall (1932, p. 80) has described this phase of the display in greatest detail in a captive bird (fig. 17). The male turned head first under the perch and held the body nearly horizontal with the wings spread and turned well up. The tail was spread and turned up with the tail wires vertical; the head and neck were extended and turned upward. The plumes were erected at an angle of 45 degrees and extended around on each side so that they formed a circle when they met anteriorly and posteriorly. Each plume was well separated from the others and stood out as a separate entity. The body movement was a slight rotary motion from side to side, making the plumes wave. This display was silent and lasted about five minutes, after which the bird returned head first to normal position.

Draffan (1978), Wagner (1938), and Crandall (1932) have recorded this species as inverting head first. Stonor (1936), Detzner (in Stresemann, 1924), Gilliard (ms), and LeCroy (personal observ.) have recorded it inverting tail first. Obviously there is variation. In either event the bird faces in the opposite direction to what it did before inverting and the position taken by the female observing the display will be of interest. The bird I observed inverting tail first came back up to the limb head first.

Paradisaea rubra: Frith (1976) described an Inverted Display in this species. The captive bird gradually leaned over a vertical branch on which it was perching diagonally with bill pointing upward, spreading and shaking his wings as he did so. When completely inverted, he spread the wings wide, vibrating them and swaying the body from side to side. This made the plumes conspicuous although they were neither spread nor

raised. He may give a soft, high-pitched *meew* or a single snap of the mandibles. At the peak of display the bird was momentarily motionless with wings fully extended on either side level with the body and vibrated very slightly and rapidly. The flank plumes were very slightly raised, but not spread and the tail was slightly depressed, both motions accenting the plumes. The male may give an occasional mandible-snap. Crandall (1937, p. 193) also described this display in captivity.

HOPPING: This is Dinsmore's (1970a) Dancing Display. I believe Hopping (or Hopping-on-the-Spot as used by Frith, 1976) better describes this posture as Dancing implies a more active display and has been used in the literature to describe the entire display sequence and various parts thereof.

In *P. apoda* this display is performed in a crouched position. The bird "slowly and rhythmically bounces and shuffles back and forth along the court with leg flexion exaggerating the vertical motion" (Dinsmore, 1970a, p. 310). The movements are slow and rhythmic and both feet are off the limb at the same time. The displaying bird gives a *click* call and sometimes a *bonk* note. This is a display given by the male with the female present.

In *P. decora* the male bounces slowly up and down in the period just before copulation. Both feet were seen to leave the perch. Occasionally the male gives loud *whick-whick* calls at this time, but he is generally silent (LeCroy, Kulupi, and Peckover, 1980).

Paradisaea raggiana salvadorii: David Gillison (personal commun.) has observed Hopping in this species. As two males dueted at the bottom of a steeply sloping display limb, a female landed on the upper part and moved down near the males. One male began to "rock." The female turned and started slowly up the limb. As the male approached "rocking" slowly, the female began to rock and they hopped slowly and in a very ritualized manner up the limb, bowing from side to side in unison as they went (fig. 18). This lasted about 30 seconds.

Another display reported by Cooper (in



FIG. 17. Inverted Display in *Paradisaea guiliebmi*. New York Zoological Society Photo.



FIG. 18. Hopping in *Paradisaea raggiana* with female leading. Photograph by David Gillison.

Cooper and Forshaw, 1977) was seen only once, when a male was displaying to a female on a horizontal branch. "After displaying in the usual manner the bird relaxed the plumes, but, with wings raised above the back, turned to face along the perch toward a female sitting about 25 cm. away. The feathers of the throat and breast he puffed out to form a round 'ball' and the head was withdrawn into this 'ball' so that only his crown and protruding bill were visible. Holding this posture he then rocked back and forth, coming toward the female so that he almost touched her with his bill." This display lasted about six seconds; then the female left. Cooper did not state whether the feet left the perch as the male rocked back and forth, and it may be that this rocking by the male alone precedes the joint hopping and bowing, as in the display above. The position of the perch, whether it is horizontal or vertical, may also influence the exact form of the display.

Clifford Frith (ms) has also described both of these components of display of captive *P. raggiana* and from the film by David Parer.

Paradisaea minor: I have been unable to find any indication of a Hopping display in this species.

Paradisaea guilielmi: Female-male encounters have not been observed in this species.

Paradisaea rubra: Frith (1976, p. 73) describes the Hopping (=Hopping-on-the-Spot) display as mechanical and slow, sometimes interspersed with "Head-peering" in which the head is rotated and its green plumage conspicuously erected. This is associated with bill-tapping, which produces an audible tick, an occasional bill click, and rapid wing vibration with slight swaying of the body. There was no female present when this display was given but it came at the end of a sequence of high intensity displays. Female-male encounters have not been observed in this species.

COPULATION: Dinsmore (1970a, p. 311) describes one mating in *P. apoda apoda* in detail: "On this occasion I saw that the male's wing next to the female was extended over her body and as he flapped his wings he held

her close alongside his body. The male also repeatedly rubbed his bill against her bill, bit at her bill, and stretched his head and neck beneath hers and rubbed his bill on the far side of her head, all as he continued to dance." This lasted for about 20 seconds before the male mounted and copulated with the female.

Paradisaea decora: Just prior to copulation the male rubs his chin and breast on the back of the female. When he mounts her his wings come down around her body and they copulate (LeCroy, Kulupi, and Peckover, 1980).

Paradisaea raggiana: I find no published description of copulation in this species. David Gillison (personal commun.) reports that after the 30 seconds of Hopping reported above, the male mounted and the pair continued to bow back and forth for another 30 seconds. Then the female turned across the limb with the male still on her back and copulation followed. The male's duetting partner and two other plumed males watched the Hopping sequence with plumes raised and crowded around the copulating birds but did not try to interfere. After copulation the female flew away and the male flew to the top of the tree and began plucking leaves.

Photos by David Gillison and a film sequence by David Parer of this species copulating show the wings around the female; in addition the film sequence shows rather aggressive bill sparring between the two birds during copulation.

Paradisaea minor: Peckover (1973, p. 11) reports that "the female is attracted to the dominant male, moves on to his display branch and then under his wing; display continues for a time, he then ceases and mounts the female." Cooper (in Cooper and Forshaw, 1977, p. 190) noted that "the male beat his wings over and about [the female] for some twenty seconds and then mounted her twice."

Paradisaea guilielmi and *P. rubra*: Copulation has not been observed.

Paradisaea rudolphi

Paradisaea rudolphi has been omitted from the above characterization of display

postures because it is poorly known and some of its behavior is anomalous. After much consideration I have come to the conclusion that it is probably not a polygynous arena displaying species but has secondarily become territorial. My reasons for this conclusion are several. In the first place no loud calls of groups of males on arenas have been recorded, nor have several males been seen displaying together. When the display has been seen in the wild (Smyth, 1970, p. 70) the male has been displaying alone in the understory with no other plumed or unplumed birds nearby. The male makes a characteristic growling noise at this time.

In November 1979, W. S. Peckover and I observed a male *P. rudolphi* near the Aiyura Agricultural Station that seemed quite territorial. The bird moved about in a complete circle perhaps 300 ft. in diameter and called in the characteristic two-toned calls of this species from high in the trees or gave loud *kow-kow-kow* calls and low growling calls from midway up in the trees. There was never any sign of another bird, either male or female, and the male moved about regularly from one spot to another within what I interpret as his territorial boundary.

On five days in October 1980, near Ubangi in the Eastern Highlands at approximately 1700 m., I watched and listened to a male *P. rudolphi* visit in succession five or six trees located in a rough circle about a quarter mile in diameter. He called and growled from high in these trees for approximately three hours, from about six o'clock each morning. Other males could be heard at a distance. Only once was a female-plumaged bird seen. It was feeding in one of the sentinel trees at a time when the male was at a distant tree, and the visit of several minutes' duration elicited no response from him. The male was also observed feeding within the territory.

Mary Stringer (personal commun. and 1979, p. 26) saw three males spaced out through a small area of remnant forest in a gorge. Apparently these territories did not include feeding areas as she and other observers have seen numbers of plumed males and unplumed birds feeding together in a

fruiting tree. Nearby a lone male was seen perching and calling in two trees about 15 m. apart.

There are several reports in the older literature of several *P. rudolphi* being seen together, and Mary Stringer (personal commun.) was told by a local man that two plumed males dance together but that when a female comes one is chased away and the other courts the female. Perhaps this latter case refers to a territorial encounter, and as several individuals of this species are known to feed together these older accounts need verification.

The female is more nearly male plumaged than in any other of the species of *Paradisaea* and may jointly defend a territory with the male, or as Thane Pratt (personal commun.) has suggested to me, may defend a territory of her own. The female (confirmed by dissection) has been shown by Crandall (1932, p. 77) to have a display in captivity in which she assumed a posture similar to that of the male but was silent. No other species of *Paradisaea* has been reported to have a female display. Also there is no great sexual dimorphism in size between males and females as there is in all of the arena displaying species of *Paradisaea* (table 1).

While there are the usual reports of unplumed birds moving through the forest together, Cooper (in Cooper and Forshaw, 1977, p. 204) reports what is unique for this species—a plumed male and a female (how identified?) feeding and moving together in the forest. Thus, there may be a period in which there is a pair bond in this species. But virtually nothing is known of incubation and feeding of the young. The two or three observations of nests record the female incubating and feeding young. The unplumed male is similar in plumage to the adult female; the adult male has a much shorter tail (table 1).

The static display that has been observed is rather like the static display of *P. guilielmi* and like it may be homologous to the Flower Display of other species. Crandall (1921, p. 113 and 1936, p. 102) describes this display in captivity. The male lowers himself backward and hangs head downward for several

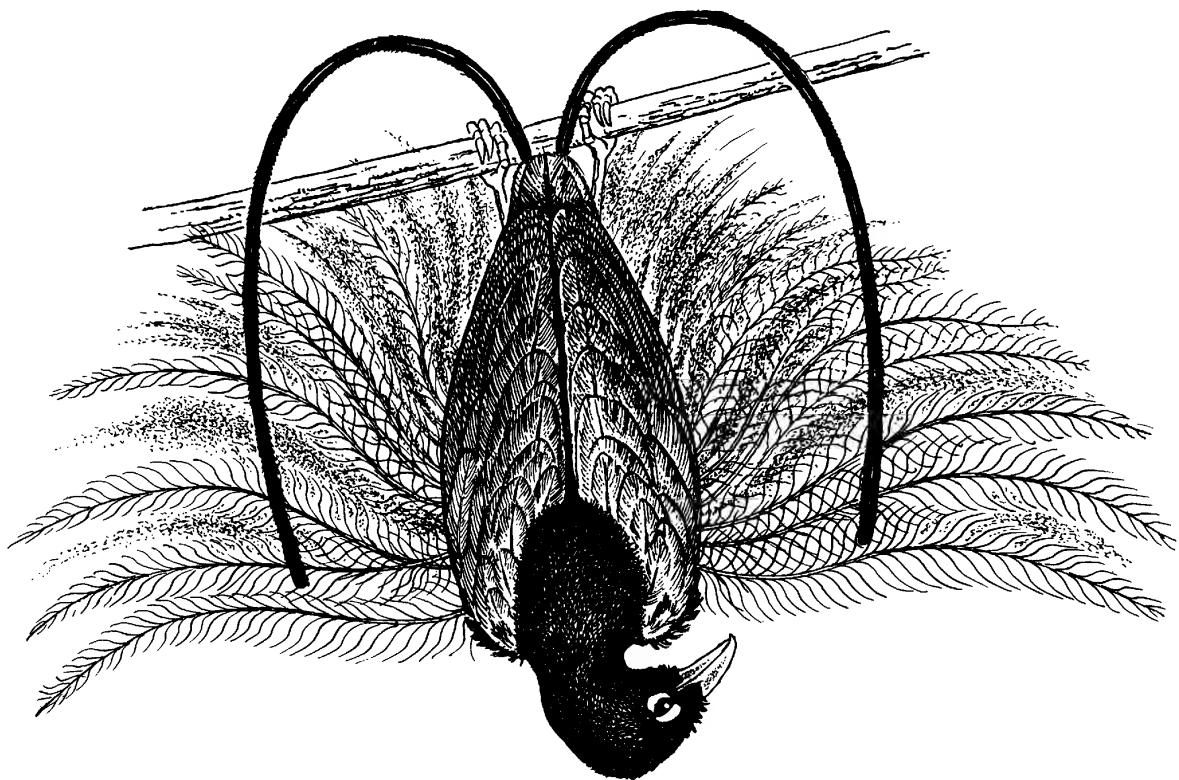


FIG. 19. Inverted Display in *Paradisaea rudolphi*. Drawing by Juan Barbaris after a New York Zoological Society Photo.

minutes without moving the feet (fig. 19). The wings are closed and the head points upward; the plumes and the abdomen feathers are spread. The tail wires rise above the plumes and then droop down on either side and the broken white eye-ring is conspicuous. The bird sways gently back and forth with the hips as a fulcrum, causing the plumes to move. According to Crandall, this display is accompanied by a low grating noise.

The female display mentioned above and described by Crandall (1932, pp. 77-78) is very similar to the above but there were of course no plumes, the tail was pressed forward between the legs and there was a rapid up and down motion, effected by bending the legs, which was never seen in males.

Both Frith (in Cooper and Forshaw, 1977, p. 206) and Gilliard (MS) mention that *P. rudolphi* assumes its inverted position by drop-

ping backward from the perch into the inverted position. The male is then facing in the *opposite* direction from that in which he was facing before inverting. No observers have yet commented on this fact or on the position of a female before the male inverts.

Frith (in Cooper and Forshaw, 1977, p. 206) reports seeing a captive female *P. rudolphi* fly to and perch above an inverted displaying male, looking down at him. This is very much like the cases reported by Drafan (1978, p. 159) for *P. guilielmi* and for *P. raggiana* by Gilliard (MS), where in each case the bird was an unplumed male. Frith does not say how the sex of the bird he observed was known. When the displaying male that Frith saw returned to its normal position, head-first, he displaced the unplumed bird from the perch above him. There is no information on copulation or precopulatory display. If this bird does prove to be terri-

torial with a pair bond, copulation may not occur at the display limb.

OTHER DISPLAY COMPONENTS

BILL-WIPING: This is not a display posture but apparently occurs as a component of display in several (and perhaps all) species of *Paradisaea*. Dinsmore (1970a, pp. 312-313) found bill-wiping to occur in *P. apoda*. We did not notice it in *P. decora*. Gilliard (MS) said there was much preening and bill-wiping in conjunction with beginning display in *P. raggiana*. "In executing the latter the bird will walk along a limb audibly pecking and wiping first one side of the bill and then the other. He does this for some time and then, back on his perch, he begins to assume the dance position." Gilliard (MS) also noted that in displaying groups of male *P. minor* "the body was held down much of the time, the bill was wiped, first one side, then the other." Ogilvie-Grant (1905, p. 438) observed bill-wiping in a displaying captive male *P. minor*. I saw an unplumed male of *P. guilielmi* bill-wiping several times just before it gave an inverted display. Frith (1976, pp. 70, 73) noted that at the beginning of display a male *P. rubra* "occasionally performs Bill-wiping," and "ritualized Bill-wiping" occurs sporadically throughout display. I have not found reference to *P. rudolphi* bill-wiping.

From the observations noted above, it seems obvious that bill-wiping is probably a regular and ritualized part of display in *Paradisaea* and it needs to be specifically looked for so that its role can be determined.

PECKING-AT-PERCH: This appears to be another ritualized display component which has been mentioned by several authors. Dinsmore (1970a, p. 312) said it occurred in *P. apoda* during a break in the display. Gilliard (MS) noted "symbolic pecking" in a *P. raggiana* male as it moved up a ladder-like vertical series of limbs "pausing here and there to peck at the hard wood of the perch with such strength that I could hear it 50 feet away. Also it pecked and pinched with its bill little knobs of wood which protruded like nail heads from the vertical limb, always wrestling rather viciously with these before

moving on." He also mentioned that on another occasion, after chasing away an unplumed bird, an unplumed bird that was in possession of a display limb, "gave a vigorous display of pecking at knobs of wood, shaking body violently and climbing up and hopping sideways down vertical part of display stage." Frith (1976, p. 73) said that near the end of the Hopping Display, a *P. rubra* male taps "the sides of the bill at its very tip sharply on the perch every few seconds while the head is rotated (Hear-peering) with its green plumage conspicuously erected. The bill tapping produces a clear tick, which is quite audible at ten metres." This is not necessarily homologous to pecking-at-perch in the other species. I found no mention of pecking-at-perch in the other species, but I suspect that it is easily overlooked.

RITUALIZED PREENING: Ritualized preening is documented by Dinsmore (1970a, p. 312) for *P. apoda* and by Gilliard (MS) for *P. minor* at the beginning of the Flower Display and for *P. raggiana* at the beginning of display, but apparently has not been noted for the other species. This ritualized preening as a part of display is not to be confused with post-display preening which has been noted for several species.

A kind of ritualized body-shaking has been noted by Gilliard (MS) for *P. minor* and *P. raggiana* but not for other species.

LEAF-PLUCKING: Leaf-plucking is an important component of display in *Diphylodes*, clearing the vegetation from above their low display courts. It also seems to be an important component in the genus *Paradisaea*. Dinsmore (1970a, p. 312) mentioned leaf-tearing in *P. apoda* in or near the display area. These were large palm leaves and the flora on Little Tobago Island in the West Indies was one to which the bird was introduced. Perhaps the bird was unable to pluck the entire leaf. On one occasion the bird carried a piece of leaf to his display limb and dropped it there; Dinsmore did not see birds eating leaves (see Frith and Frith, 1979). This activity appeared to Dinsmore to be associated with display but not an integral part of it; it most often occurred after a brief visit by a female prompted a partial display. Lu-

ban (in Baker, 1923, p. 297) had earlier reported that on Little Tobago "A queer action of the males . . . is their snapping off of tiny twigs of leaves. This is usually from their 'dancing' trees."

We observed leaf-plucking by a male *P. decora* on several occasions (LeCroy, Kullupi, and Peckover, 1980). This most often occurred during lulls in display and with only one male present but did occur once during a brief display. The birds always plucked the leaves from above a main display limb.

Frith and Frith (1979) have recently reported leaf-plucking and leaf eating by captive *P. raggiana*, and in Varirata National Park near Port Moresby I have seen that the area above a display limb was almost entirely bare of leaves.

Gilliard (1969, pp. 233, 234) noted two instances of leaf-plucking by *P. minor*. Once a male displaying with a number of other males interrupted display and moved away 6 feet to violently rip off large leaves and drop them. On another occasion a single male, after landing in a display tree, violently ripped off leaves and held them a few seconds before dropping them.

Frith (1976, p. 73) saw a male *P. rubra* clearing a new display perch by plucking and dropping leaves. He believes that the activity may have originated as displacement activity but now serves to create display perches and keep the area around them clear. I agree that this seems a likely origin of the habit. There are several references in the literature to the morning sun hitting display limbs, and it may be that leaf-clearing facilitates this, although we saw no correlation between sun and display activity in *P. decora*.

BUTTERFLY DANCE: Stonor (1936, p. 1181) in writing of *P. guilielmi* in captivity noted: "Next follows the third and last part of the display, during which [the male] hops from perch to perch, performing a sort of dance, fluttering the wings and occasionally spinning round in small circles; as in the first stage, no use is made of the plumes." This display followed the inverted display and there was no female (or other male) present. I have not found anything comparable in other species. I consider the preliminary display

observed by Frith (1976, p. 73) in *P. rubra*, and called a Butterfly Dance by him, more likely to be a Charging Display.

SUN-BATHING: Frith (1976, p. 74) first called attention to this phenomenon in his article on *P. rubra*. He said that captive males of this species sunned for long periods in direct sunlight in a "peculiar pose with one wing drooping, the body leaning away from the sun and the head held high with bill pointing upward or tilted to one side." Gilliard (MS) noted a similar display in a captive individual (fig. 20): "The tufts on the forehead and the green shielding on the sides of the lower head were elevated and flexed as the bird struck one pose or posture after the other. Such posturing was executed after the male had scaled the thin trunk of a heavily leafed tree. At the top of the climb with the head protruding into the sun above the low crown, it would suddenly stiffen into the oddest sorts of positions. Often the head was thrust off to one side and this unnatural position was held for seconds. At other times it leaned uncommonly far back and lofted the head and neck still farther as though drawn by a cruel check rein"

Gilliard (MS) noted in *P. raggiana* that: "Sometimes during the quiet part of the day silent males assumed rather grotesque positions, partially hanging over the limbs with the chest and head held downward and fairly motionless for long seconds." This may not correspond to the above and could conceivably be a sleep posture. I have seen a young Red-footed Booby sleeping in this position. However, on another occasion (1969, p. 226) he noted: "As a general rule males sat on their private courts or on semi-hidden perches nearby for many hours per day. They sat quietly except for occasional calling and not infrequently as they sat they would lean backward or to the side so far out of balance that they appeared to be dying."

SEED REGURGITATION: Several species of *Paradisaea* have been seen to regurgitate seeds while on the display limb. It has been reported for *P. apoda*; Gilliard (unpublished notes, 1958) and Fred Truslow saw birds regularly regurgitate seeds as they sat on the main display limb between bouts of display.



FIG. 20. Sun-bathing in *Paradisaea rubra*. Photograph by E. T. Gilliard.

The bird drew back its head and kept the posture for about three seconds, then began working open mandibles. After a few seconds, a seed came flying out in a gentle arc. Dinsmore (personal commun.) saw this species regurgitate seeds of Gumbo Limbo, *Bursera simaruba*.

Fred Shaw Mayer told Gilliard (unpublished notes, 1959) that captive *Paradisaea raggiana* were fed on oily pandanus seeds, which they swallowed whole. They later regurgitated the seeds.

W. S. Peckover discovered that *P. decora* on the display limb regurgitates seeds of

Medusanthera laxiflora, a food plant. On investigation we found that there were numerous other seeds of that species beneath the display tree. Most display trees we saw had food trees of this species and others growing beneath them, doubtless a result of seed regurgitation. There is no evidence that seed regurgitation is an element in actual display, but it may function to cut time spent searching for food, thus allowing more time for display. And W. S. Peckover (*in litt.*) suggested that it may serve as an added attraction to females.

CALLS

Calls are extremely difficult to analyze as no two workers record them in the same way. Therefore, the following is only a brief attempt to group calls.

All species of *Paradisaea* have had one or two types of crowlike calls recorded. In addition, there are shrill *kii* or *quee* calls recorded for *P. apoda*, *P. raggiana*, and *P. minor*. *Paradisaea guilielmi* is reported also to make a popping call "like Chinese fire-crackers" (Draffan, 1978, p. 58). A growling call has been reported for *P. minor* (Gilliard, unpublished notes, 1958), *P. decora*, *P. raggiana*, *P. rudolphi*, and *P. guilielmi* (personal observ.). A whiplike call has been reported for *P. decora*, *P. minor*, and *P. guilielmi* (personal observ.); a mewing call for *P. raggiana* and *P. rubra*; and a click call for *P. rubra* and *P. apoda*. The duetting calls of *P. decora* are probably homologous to the bungle-like calls of *P. raggiana* and *P. apoda* mentioned by Gilliard (MS) and to the bubbling duet I heard given by *P. guilielmi*, Frith (1976) mentioned a "weep," a mandible snap, and Bill-click-call for *P. rubra* and Dinsmore (1970a) a "Cugich" call for *P. apoda* which do not seem to have counterparts in other species.

DISPLAY BY UNPLUMED MALES

Display by unplumed males has been reported for most species of *Paradisaea* and probably occurs regularly. There is the possibility that on occasion these are molting males, but molting birds in captivity do not

display. Also these birds frequently lack yellow or green on the head and have no tail wires. They seem to move about regularly in bands or "drones" as Gilliard (MS) called them.

The unplumed males may display in the absence of plumed males and may reoccupy traditional trees when plumed males are shot as suggested by Healey (1978a, p. 154): "Some subadult males [of *Paradisaea minor*] may mate at display-trees abandoned by adult males: at Tabibuga I observed two subadult males displaying in early June with no adult males but several female-plumaged birds nearby. This indicates that display trees are not necessarily abandoned if all mature males are shot. Though females may not mate with subadult males when mature males are present, they may do so where display trees are widely spaced and mature males locally rare."

Gilliard (1969, p. 226) saw that an unplumed male of *P. raggiana* may obtain a display limb after the owner was shot: "Not knowing of the shooting, I sat under its display space—a sloping limb—for three mornings waiting for the distinctively-plumed owner to return. Other adult males in the arena did not visit this limb, but three days after the shooting a young male still in female dress investigated it. It flew in quietly and perched at one end of the limb, then after a few seconds it jumped onto the main display space, crouched, and began thumping its wings overhead, exactly as in the adult male."

Gilliard (MS) spoke of "drones" of displaying unplumed male *P. minor* around displaying plumed males, and we (LeCroy, Kullupi, and Peckover, 1980) several times saw groups of unplumed *P. decora* males displaying to, and mating with, females in the presence of a displaying plumed male. Wallace (1869) noted unplumed male *P. apoda* displaying. Probably unplumed males of all species (except *P. rudolphi*?) do so regularly.

It is probable that the brightly colored plumes serve as a signal to males to gather and display. D'Albertis (1876) has reported that people in the Fly River area and on the

Aru Islands suspend plumes of *Paradisaea* in a tree to which they wish to attract males, and Goodfellow (1910) mentions a similar practice on the Mimika River. Unplumed males may be allowed around the arena because they have no plumes, and it may be that only a small percentage of the males in the population is plumed at any one time.

Inhibition of plume development in subordinate males cannot be ruled out. (Steinbacher, 1938, mentions that dominated birds may lose their sexual plumage.) The estimate of the number of years required for a male *Paradisaea* to acquire plumes is based either on stages of plumage in museum specimens (which may reflect hormone levels more closely than age) or on the age at which captive birds acquire plumes (which may be a minimum age as they are usually alone in the captive situation and therefore without a dominance framework). Recruitment into the dominance framework in the wild may permit plume development and give the bird an opportunity to become the dominant male.

EVOLUTION WITHIN THE GENUS *PARADISAEA*

Most recent authors (Bock, 1963; Gilliard, 1969; Diamond, 1972; Frith, 1976) have considered the genus *Paradisaea* to be closely related to *Diphylloides* (including *Cicinnurus*, see Diamond, 1972). I agree and believe that various elements in the display of *Paradisaea* support its close relationship to *Diphylloides*. The use of a vertical or near vertical limb in displays of *P. rubra*, *P. raggiana*, *P. decora*, and perhaps other congeners, and leaf-plucking over the display limb are similar to elements of display in species of *Diphylloides*. *Paradisaea* and "Cicinnurus" have several display postures in common; see especially the "first stage of display" figured by Ingram (1907, p. 226), the inverted display described by Bergman (1957b), and the zigzagging display described by Gilliard (1969, p. 197). The crowlike call of *Paradisaea* is very similar to that of *D. regius* and fairly similar to that of *D. magnificus* (Diamond, *in litt.*). Also *Paradisaea*

and *Diphylloides* are the only two genera in the family that have the central tail feathers of males modified into wirelike (ribbon-like in *P. rubra* and *P. rudolphi*) structures (Diamond, 1972).

Gilliard (1969) proposed that the ancestors of birds of paradise were arboreal and monogamous and that polygynous arena species evolved and were different morphologically but behaved like semispecies in that they excluded each other geographically and ecologically. A result of this exclusion was that some of the arena birds were displaced downward to display on the forest floor. *Diphylloides* was one such line and as such would be more recent and highly evolved than arboreally displaying *Paradisaea*.

Frith (1976) accepts this direction of evolution and further believes *P. rubra* to represent a possible intermediate stage between communal display and individual display. However, his reasons are based partly on observations of captive birds whose displays likely were affected by the presence of a human observer. It seems to me that increased dispersal during display when an observer is in the cage and indications that the bird is descending toward forest floor are both artifacts of captivity. Gilliard (MS) noted that a male *P. raggiana* displaying in the wild moved from the main to a peripheral display limb when disturbed by an observer—the logical reaction to disturbance. And both Gilliard (in Greenway, 1969) and Bergman (in Gyldenstolpe, 1955) only saw *P. rubra* in the exposed tops of trees in the wild.

I do not think we are yet in a position to make a statement as to the direction of evolution. We are not certain, for example, that there is no pair bond in *Diphylloides*. And it could be argued that because barring is present in most female birds of paradise, this is the primitive condition and *Diphylloides* is thus primitive. *Paradisaea* could then be derived from ancestors in which females are barred through intermediates, such as *P. rudolphi*, in which females are barred on the abdomen. But barring in females may be independently evolved and convergent, and as *P. rudolphi* seems anomalous in many facets of its display, it seems premature to propose

that species as the primitive species in the genus.

Among the remaining species of *Paradisaea*, *P. rubra* appears to be the least specialized in terms of plume development. It has probably also been isolated the longest on the islands of Waigeu and Batanta. Frith (1976) has pointed out that posturing on a vertical limb was the most developed part of the display he observed, and movement of the highly developed feathers on the head was an integral part of display. In each of these respects *P. rubra* is more similar to *Diphyllodes* than to other species of *Paradisaea*. The iris of *P. rubra* is brown, as in *Diphyllodes*. On the other hand, the display repertoire of *P. rubra* has most if not all of the elements present in displays of the other arena species of *Paradisaea*.

The three similar species, *P. apoda*, *P. minor*, and *P. raggiana*, hybridize rather freely whenever they are in contact; and the static Flower Display, which I believe to be the species-recognition signal in these non-pair-forming birds, is similar in these three taxa. I believe they should be considered a superspecies, *P. [apoda]*, as Diamond (1972, p. 316) has suggested. [I am defining superspecies as "a group of entirely or essentially allopatric taxa that were once races of a single species but which now have achieved species status" (Amadon, 1966; Short, 1969) and semispecies as populations that are essentially allopatric but that show some hybridization in areas of overlap. "Semispecies are one type of allospecies comprising a superspecies" (Amadon, 1966; Short, 1969, p. 90). The use of brackets to designate a superspecies follows Amadon, 1966.] The male-male displays of *P. apoda*, *P. minor*, and *P. raggiana* differ only in detail, and I believe these differences are more apparent than real and that as our knowledge increases so will our understanding of the similarities. The plumed males and adult females have a yellow iris in all three taxa. These three semispecies probably evolved on the Aru Islands, in northern New Guinea (or on the Vogelkop), and in southeastern New Guinea, respectively, and have subsequently spread until they encircle New Guinea from

sea level to slightly over 1500 m. where suitable forest occurs.

Paradisaea decora is morphologically similar to *P. [apoda]* and should be included in the superspecies. Plumed males and adult females have a yellow iris, and the Flower Display is similar to that of *P. [apoda]* but not quite so highly developed. *Paradisaea decora* display differs mainly in the importance of Male-male Duetting in setting up the male hierarchy, but Male-male Duetting occurs in other species and may prove to be common. The females have faint barring or speckling on the abdomen.

Paradisaea guilielmi undoubtedly evolved in isolation on the Huon Peninsula at a time when it was separated from the central mountains by a water barrier. Reinvasion of the area by *minor* from the northwest and *raggiana* from the southeast has perhaps driven this species to higher elevations. However, both *P. guilielmi* and *P. raggiana* occur together in the Saruwaged Mts. at about 450 m. (personal observ.). *Paradisaea guilielmi* is known to hybridize in the wild with both *P. minor* and *P. raggiana*. The inverted display of *P. guilielmi* is undoubtedly an isolating mechanism. Gilliard (1969, p. 256) believed that inverted display was probably derived separately in *P. guilielmi* and *P. rudolphi*, and I agree. As there is some evidence of inverted display in most species, it is not hard to imagine its enhancement in these two species independently. Crandall (1932, p. 80) mentions that the plumes of *P. guilielmi* were "erected at an angle of about 45°" on the ventral side of the bird and spread anteriorly and posteriorly to form two semicircles which met to form a complete circle around the breast and abdomen of the inverted bird. Stonor (1936, p. 1181) said that during display in *P. rudolphi*, "the plumes are spread out in the form of a fan, but are not pointed forward to the same extent as in *Trichoparadisea* [= *P. guilielmi*]." It would be interesting to study the musculature of the display plumes to see how birds giving an inverted display differ from those in which the plumes are raised above the back, and whether *P. rudolphi* and *P. guilielmi* differ in this respect. Plumed

males and females of both species have the iris dark as in *P. rubra*, but the plumed male of *P. rudolphi* apparently has a navy blue iris.

As Gilliard (1969) has pointed out, the number of intergeneric and interspecific hybrids known from the wild in the Paradisaeidae indicates that these birds are much more closely related genetically than the morphology of the males would imply and that arena behavior allows selection to act very rapidly on the species, particularly on the males. Thus the display postures that serve as isolating mechanisms assume great importance in the non-pair-bonding species. It is especially in these that we find the most diversity within *Paradisaea*, and where two species meet the displays that serve to prevent interbreeding are most different. But even so, inverted versus noninverted display has not served completely to prevent hybridization, as wild hybrids between *P. guilielmi* and *P. raggiana*, *P. guilielmi* and *P. minor*, and *P. raggiana* and *P. rudolphi* are known. It would be of great interest to know exactly where these hybrids were found and which species provided the male and which the female parent. If males tend to occur at higher altitudes than females within a species' range, as they do in some species (Diamond, 1972), then it seems likely that the male parent was a member of the *P. [apoda]* superspecies and the female a member of the species with inverted display. Thus a female at the lower altitudes of her species' range and ready to mate might occasionally respond to the display of *P. [apoda]* males in the absence of males of her own species.

Stonor (1936) has discussed evolution within the genus *Paradisaea* and decided on the basis of captive displays and feather structure that *Uranornis* (=*P. rubra*) branched off from the ancestral stock earliest followed by *Paradisornis* (=*P. rudolphi*) and *Trichoparadisea* (=*P. guilielmi*) stock which later gave rise to the two species with inverted display. *Paradisaea decora* next branched off earlier than the remaining species.

My interpretation based on the analysis given in this paper is that within the genus

Paradisaea, *P. rubra* is closer to the ancestral stock, has the most generalized display, and does not spread its plumes. I envision development in two directions from a *rubra*-like ancestor (which may have been widespread in New Guinea). In one direction *P. guilielmi* may have evolved. Some of its postures are similar to those of *P. rubra*, particularly the Wing Pose; and display of the green head feathers is pronounced in both species. *Paradisaea rubra* also has a well-developed Inverted Display although it is given on a near-vertical limb and is not as highly developed as that in *P. guilielmi*. Spreading of plumes ventrally would have developed independently of plume spreading in the other species.

Along another line, *P. [apoda]* probably developed by accenting the upright poses in display and raising the plumes over the back in a cascade. As mentioned by Frith (1976, p. 75) the wing position of *P. rubra* most closely resembles that in *P. minor*. The depression of the tail (Frith, 1976, p. 75) seems to me to function strictly as a counterbalance in those species which raise the plumes over the head. Thus, it would not be expected to occur in *P. rubra*, *P. guilielmi*, and *P. rudolphi*, nor does it occur in *P. decora*, where the plumes are not thrown so far forward.

Paradisaea rudolphi may either be the most primitive member of the genus (its possible pair bond behavior having been retained from an ancestral form), or it may have diverged from the *Paradisaea* line more recently (its probable territoriality and the barred plumage of the female being derived characters). Most authors agree to a close relationship between *Diphyllodes* and *Paradisaea*, and Diamond (1972) has pointed out that the red and yellow pigments present in *Diphyllodes* have counterparts in most species of *Paradisaea*. *P. rudolphi* is unique in having blue and black plumage. The bird's inverted display is also different from that of *P. guilielmi*, the flank plumes being spread fanlike across the lower abdomen and not angled at all. These may all be secondary adaptations evolved in response to competition with *P. raggiana* across its range. Dia-

mond (*in litt.*) has suggested that perhaps "*P. rudolphi* is the old eastern member of the *Paradisaea* superspecies, and diverged rapidly as well as was displaced altitudinally when its range was overrun by the western population that became the *minor-raggiana* line." I agree that this may be the case.

The short plumes of *P. rudolphi* may not be a primitive condition. The species is not known to have a Wing Pose, Charging Display, or Zigzag Display, all of which are male-male displays at the arena. If, as I have hypothesized, the plumes in *Paradisaea* have developed in response to male-male interactions, they are perhaps being lost in this species. Furthermore, if character displacement is involved as Gilliard (1969) thought, then shorter plumes would be at a selective advantage in this species (as well as in *P. guilielmi*) because the two species are competing with the sympatric long-plumed *P. minor* and *P. raggiana*.

Paradisaea rubra is smaller than members of the *P. apoda* superspecies but is not smaller than *P. guilielmi* and *P. rudolphi* (see table 1). I believe that small size may prove to be a primitive character in *P. rubra*. *Diphyllodes* certainly is small, and Bock (1963, p. 122) found that the group of genera including *Diphyllodes* had the least specialized skull within the Paradisaeinae. However, he stresses that with the evidence at hand it is impossible to tell whether this un-specialized skull is truly primitive. Character displacement may be involved in the smaller size of *P. guilielmi* and *P. rudolphi*.

Frith's (1976) statements deserve comment. He said that the small size of *P. rubra* occurs despite the fact that it is confined to small islands "where individuals tend to be larger in size of body (Mayr, 1963)" and that "the larger size of other members of the genus could be because they extend higher altitudinally than *P. rubra*, birds at higher altitudes having been proven to be larger in New Guinea (Rand, 1936)." Mayr (1963, p. 319) said: "In view of occasional misunderstandings in the literature, it is important to emphasize 'that the validity of the ecological rules . . . is restricted to intraspecific variation . . .' (Mayr, 1956)." Altitudinal varia-

tion in body size is also intraspecific (Rand, 1936). Thus these general ecological rules cannot be applied interspecifically in *Paradisaea* where gene exchange is minimal or nonexistent and evolutionary pressures differ.

EVOLUTION OF NON-PAIR-BOND POLYGYNY

The similarities are striking between non-pair-bonding polygynous arena-displaying birds of paradise and birds in totally unrelated families but with a similar social structure. The studies by Chapman (1935), Gilliard (1959), Sick (1967), and especially Snow (1976 and earlier papers listed therein) and Foster (1977 and personal commun.) on New World manakins (Pipridae); the studies by Gilliard (1962) and Snow (1976 and earlier papers) on cotingas (Cotingidae); the studies by Shepard (1976) on Ruffs (Scolopacidae); the studies by Kruijt and Hogan (1967) on Black Grouse (Tetraonidae); and others too numerous to mention all show that these diverse species have evolved basically very similar solutions to the problems associated with maximum reproductive output. The six characteristics of arena birds which I discussed earlier apply to the above: loud calls by males on the arena (mechanical noises sometimes substituted), extreme sexual dimorphism in plumage, males considerably larger than females, few males in adult plumage compared with the number of unplumed males and females seen, groups of males displaying for long periods of the year whether or not females are present, and the species frequently but not always belonging to speciose genera. Male-male displays differ from female-male displays and many of the above authors have commented on these differences. In one species, at least, there is a proven male-male bond between two or more males on one display perch or court (see Foster, 1977). These similar developments related to the social systems in unrelated birds raise many questions.

A number of theories have been put forward to explain extreme sexual dimorphism and polygyny in birds. The earliest was Dar-

win's (1871, p. 916) theory of sexual selection about which he said, "The sexual struggle is of two kinds; in the one it is between individuals of the same sex, generally the males, in order to drive away or kill their rivals, the females remaining passive; whilst in the other, the struggle is likewise between individuals of the same sex, in order to excite or charm those of the opposite sex, generally the females, which no longer remain passive, but select the more agreeable partners."

With few exceptions, bird of paradise behavior (and that of other arena-displaying species) has been interpreted in terms of Darwin's second kind of sexual selection—females choosing the most "attractive" male. Crandall (1936, p. 88) approached a different interpretation when he questioned the term "courtship" before "display" and implied that he felt that courtship displays were primarily for the female but had spread into male rivalry situations, albeit still related to reproductive processes. "So now we come again to Darwin's theory of Sexual Selection—with a twist. For instead of carefully selecting the male that strikes her as the handsomest, it seems to me that the female acts from an irresistible impulse to accept the one that approaches most nearly the highest standard of her race. Thus would the chief principal of Darwin's thought be supported: the finest, as well as the most vigorous, would be certain of finding mates, and the species would continue in all its glory."

In *Paradisaea decora* we saw no evidence that the female made any kind of mate selection (LeCroy, Kulupi, and Peckover, 1980). The plumed males spent many hours displaying among themselves, with and without unplumed males being present. In so doing they presumably set up and maintained a mating hierarchy among themselves—chasing unplumed males away, or at least to the periphery. That this dominance hierarchy worked was shown by the disappearance of all but one other plumed male (the Male-male Duetting partner) when a female appeared, and by this male's acquiescence to the dominant male in the later stages of display to the female. This also occurs in *P. raggiana* (see above) as well as in *Chiroxiphia linearis*

(Foster, 1977) and will probably prove to be widespread in arena-displaying species. In *P. decora* the female appeared to come to a particular limb near the main display limb—a locality of high stimulation presumably, and which male was displaying seemed unimportant to her as she mated with unplumed males as well as with the displaying plumed male. In the literature most displays of *Paradisaea* in the wild are of both plumed and unplumed males; but the few observations of copulations in the wild do not conflict with this interpretation.

I think that the importance of setting up the male-male dominance hierarchy in arena-displaying birds has not been sufficiently stressed previously and that the plumes have primarily evolved in response to male-male pressures. Secondarily the plumes have become involved in the display to a female. The female ready to mate may be drawn to the arena area by the vocalizations and movements of the displaying males. But it seems likely that she is not attracted to any particular male but to a locality (or localities) within the arena, which may or may not be traditional, there to mate with whichever male has acquired that display space. A number of the authors cited above who have worked with marked birds have commented that most of the copulations go to the male(s) on the central court(s). If the female is indeed attracted by the vocalizations and movements of the males then it seems logical that this attraction would be greatest at the center, and that the dominant male or males would hold this position.

If one accepts the hypothesis that the dominant male is also superior in fitness, and if it proves to be generally true in arena-displaying birds that most copulations go to the dominant male, then essentially only his genes would be passed on to the next generation, allowing for rapid evolution in the male line. Selection on females would not occur in the display situation, the males mating with any female in breeding condition. Natural selection would act on the females in the context of their ability to raise young that reproduce.

How can a polygynous system such as this

develop? There are many theories concerning the development of polygyny, most having to do with territorial birds that have more than one mate, either simultaneously or sequentially, but within the territory held by the male and with the development of a pair bond of greater or lesser duration.

Trivers (1972) believes that the development of polygyny has to do with the investment each sex has in its offspring. As female investment becomes more and male investment less there will be an increased selection among males for more frequent matings; i.e., females will tend to be in short supply and will be competed for, and ecological factors will contribute to the amount of parental investment. This also implies some choice by the female to protect her investment and avoid mating with an inferior male. But this theory only applies in situations where a large proportion of the population of males and females is breeding and there is some sort of pair bond. In a situation such as that in *Paradisaea* where there is polygyny without a pair bond and males do not defend individual territories in which a female rears the young, it is not necessary to have female choice to produce the extreme sexual dimorphism and elaborate displays seen, as discussed above.

If this sort of system develops only in non-territorial birds we might ask what the advantages of such a non-territorial polygynous system would be.

Verner and Willson (1966) propose that the "polygyny threshold" occurs when there is a sufficient difference in quality between male territories that a female could rear more offspring on a better territory without the help of the male than she could on a poorer territory with the resident male's help. This may be as much or more a result of population density as of food availability, forcing males into marginal territories. But these authors say that the adaptive basis of non-pair-bonded polygyny eludes them.

Emlen and Oring (1977) introduce the "operational sex ratio" and define it as "the average ratio of fertilizable females to sexually active males at any given time," and they discuss the degree to which environ-

mental factors control access to and defense of mates. Under their category of male dominance polygyny they include cases in which males do not directly defend females, or resources necessary to them, but the males sort out among themselves their relative positions of dominance. Females choose males primarily on the basis of male status.

Emlen and Oring (*op. cit.*) state that "communal displaying is frequent among species in which the male is totally emancipated from parental care and the *environment provides little potential for resource or mate control.*" In such cases direct male-male encounters may occur and a dominance hierarchy be set up among the males. Under such a system a high-ranking male should benefit by joining a communally displaying group, but they ask why a subordinate male should join such a group. Presumably the strength of the stimulus is enhanced by concentration of displaying males—the larger the aggregation the more attractive it becomes to females—and "low-ranking males will be expected to adopt alternative, cryptic, or satellite strategies for obtaining females within the communal display areas rather than avoiding male aggregations altogether." This seems to be exactly what has happened in *P. decora*, where subordinate, unplumed males are usually chased by the plumed males, but during the height of display by the dominant male, in which the dominance is sufficiently strong to cause other plumed males to leave the tree or sit in silence, unplumed males slip in and copulate with the female. Whether these copulations are successful or not is another question. Presumably they could not often be or the hierarchy would break down. It is perhaps also significant in this regard that the unplumed males mated only with the female in the central position near the displaying plumed male. Several times a second female was present and occasionally solicited from another limb. The unplumed males did not attempt copulation with her although on one occasion the plumed male did copulate briefly with the second female on the other limb immediately after copulating with the central female.

It is interesting to speculate on the possibility that all of the males in a clan are related. If this were true then occasional successful matings by unplumed males, or by plumed males lower in the hierarchy, might be tolerated by the dominant male(s) as a kind of kin selection. But Foster (1977) provides strong arguments against kin selection in such cases. Proximity of the unplumed males to the display arena provides them with a better opportunity of being incorporated into the hierarchy when a dominant bird disappears. The time spent in what Gilliard (ms) called a "drone of males" might serve as a kind of apprenticeship, and Foster (1977), Snow (1976), and others have discussed the potential advantage, in evolutionary terms, to an individual serving such an apprenticeship.

Emlen and Oring (1977) further maintain that if the females are asynchronous in their sexual receptivity, the operant sex ratio becomes skewed and then lek systems develop where males remain sexually active over long periods of time and set up a relatively stable hierarchy. Display areas develop for the sole purpose of attracting females for mating and after mating they leave the area and nest and rear the young alone. To this extent *Paradisaea* exactly fits their description of a lek bird. But I see no evidence in *Paradisaea* that sexually receptive females "sample" numerous males before selecting a mate." In other words, the evidence suggests that the sexual selection involved is Darwin's first kind—male-male selection with the female remaining passive in terms of choosing a male. Females would benefit from the long period of male display, and presumably of sexual readiness, as re-nesting by females might be attempted over a much greater period of the year as long as food supplies are adequate.

That males could not control resources within a territory to support a female and young is indicated by the fact that *Paradisaea* is largely frugivorous (as is also the case with most, if not all, of the cotingas and manakins referred to above), and fruit ripening on any one tree at any one time would cause a superabundance of food in that locality.

But fruit trees may be scattered in the forests and females and/or young males are often seen feeding in groups moving through the forest. Defense of such an ephemeral food supply by males would not appear feasible, and there is no indication that females defend a territory either.

Emlen and Oring (1977) hypothesize that "all cases [of lek mating systems] will be typified by a fairly long breeding season, a heavily skewed operational sex ratio, and by the inability of individual males to economically control or monopolize the resources essential for female acquisition." *Paradisaea* fulfills all of these requirements.

I have not discussed the possibility that females of *Paradisaea* are polyandrous; i.e., that they have a succession of male partners in any one breeding season. Certainly they are in the sense that unplumed males mated with females in the arena of *P. decora*, followed by a plumed male mating with the same female. If these matings produce offspring, if females mate with more than one male in the dominance hierarchy, or if that hierarchy shifts, then these birds might be considered polygamous (males are polygynous and females are polyandrous) as suggested by Peckover (1973). Even so, it would be a facultative polyandry on the part of the female, dictated by the dominance system of the males. Given our present state of knowledge—we do not know, for example, whether a female mates more than once to produce a clutch—such a possibility can only be mentioned.

Two additional interesting ideas are relevant here. One, brought to my attention by Bertram Murray (personal commun.), is that there is some evidence in chickens (Compton et al., 1978) that sperm from the last rooster to mate with a hen fertilize the eggs. I have been unable to find any information concerning whether a sperm storage vesicle such as occurs in chickens might also occur in birds of paradise. If it does, then the copulations by unplumed male *P. decora* would not be likely to fertilize the egg(s).

Smith (1979) has proposed another hypothesis in relation to the polygynous mating system of Fallow Deer (*Dama dama*). He

states that inbreeding may be selected for in this species, in which the dominant male does all the mating, even over a period of several years, and females bring their daughters to the mating area where their father is dominant. This might occur, he hypothesizes, if the initial deleterious effects of increased homozygosity do not become excessive and if these deleterious alleles are eliminated and a new balance struck at a low level genetic load. Even so, he states that this would require altruistic behavior by the female in producing fawns with a somewhat greater genetic load than outbreeding would produce, but that this would be offset by an increase in inclusive fitness in the closely related population. Such ideas cannot be discussed in relation to *Paradisaea* until we have some information on behavior of individual birds and on relatedness of birds in the arena.

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